Factors influencing the marine spatial ecology of seabirds: Implications for theory, conservation and management

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Abstract

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Seabirds are wide-ranging apex-predators and useful bio-indicators of marine systems. Nevertheless, changes are occurring in the marine environment, and seabirds require protection from the deleterious effects of climate change, fisheries, pollution, offshore development, introduced predators and invasive species. The UK supports internationally important populations of seabirds but also has vast wind and wave resources, therefore understanding how seabirds use the marine environment is vital in order to quantify the potential consequences of further exploiting these resources. In this thesis I first describe the range of wave energy converting devices operational or in development in the UK, and review the potential threats and benefits these developments may have for marine birds. I then synthesise data from colony-based surveys with detailed information on population dynamics, foraging ecology and near-colony behaviour, to develop a projection model that identifies important at-sea areas for breeding seabirds. These models show a positive spatial correlation with one of the most intensive at-sea seabird survey datasets, and provide qualitatively similar findings to existing tracking data. This approach has the potential to identify overlap with offshore energy developments, and could be developed to suit a range of species or whole communities and provide a theoretical framework for the study of factors such as colony size regulation. The non-breeding period is a key element of the annual cycle of seabirds and conditions experienced during one season may carry-over to influence the

next. Understanding behaviour throughout the annual cycle has implications for both ecological theory and conservation. Bio-logging can provide detailed information on movements away from breeding colonies, and the analysis of stable isotope ratios in body tissues can provide information on foraging during the non-breeding period. I combine these two approaches to describe the migration strategies of northern gannets *Morus bassanus* breeding at two colonies in the north-west Atlantic, revealing a high degree of both winter site fidelity and dietary consistency between years. These migratory strategies also have carry-over effects with consequences for both body condition and timing of arrival on the breeding grounds. Finally, I investigate the threats posed to seabirds and other marine predators during the non-breeding period by collating information on the distributions of five different species of apex predator wintering in the Northwest African upwelling region. I describe the threat of over-fishing and fisheries bycatch to marine vertebrates in this region, and highlight the need for pelagic marine protected areas to adequately protect migratory animals throughout the annual cycle. In summary, the combination of colony-based studies, bio-logging, stable isotope analysis and modelling techniques can provide a comprehensive understanding of the interactions between individuals and the marine environment over multiple spatial and temporal scales.

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Chapter 1:
General introduction

1. 1 INTRODUCTION

While each of the chapters presented in this thesis has been written as a separate piece of research, and can therefore be read in isolation without the need for cross-reference, it is intended that in combination they provide a better understanding of the marine spatial ecology of seabirds and the threats they face at-sea. In this general introduction I will briefly establish the key themes of the thesis and outline the rationale behind this project, before highlighting the main aims of each chapter.

Seabirds as indicators of marine systems

Seabirds are wide-ranging predators, near the apex of most marine food chains, well monitored at breeding colonies, garner considerable scientific and public interest, and as a result act as useful bio-indicators of marine systems (Furness and Camphuysen, 1997). Nevertheless, there are also shortcomings to using seabirds in this way (Durant et al., 2009); their position at the top of food chains can buffer change, such that correlations between two variables may not be causative (Votier et al., 2008a, but see Luczak et al., 2011); produce temporal lags in the response to change (Thompson and Ollason, 2001); or individuals may be flexible in their response to change (Grémillet and Charmantier, 2010).

Seabird research has historically focused on colony-based studies because, as central-place foragers constrained to return to the nest during the breeding event, seabirds are easily accessed during the breeding season (e.g. Mitchell et al., 2004). These studies

have proven vital in expanding our understanding of seabird ecology, and elucidated the drivers of coloniality (Ashmole, 1963, Lack, 1966, Furness and Birkhead, 1984, Lewis et al., 2001); life history theory (Frederiksen et al., 2005); population ecology (Tavecchia et al., 2007, Tavecchia et al., 2008, Votier et al., 2008b); predator prey dynamics (Oro et al., 2006, Votier et al., 2008c); and individual specialisation (Woo et al., 2008).

Nevertheless, while seabirds are well monitored and protected at their breeding grounds they spend most of their life at sea, where they are less well studied and afforded little statutory protection from a diverse range of anthropogenic pressures including; offshore development (Gill, 2005, Inger et al., 2009); climatic change (IPCC, 2001, Pounds and Puschendorf, 2004, Thomas et al., 2004, Harley et al., 2006, Grémillet and Boulinier, 2009); commercial capture fisheries (Pauly et al., 1998, Lewison et al., 2004a, Votier et al., 2004b, Worm et al., 2009); and pollution (Islam and Tanaka, 2004, Votier et al., 2005, Votier et al., 2008b). To understand the responses of wide-ranging seabirds to these potentially disparate anthropogenic pressures, requires an understanding of how seabirds interact with the marine environment (Louzao et al., 2009).

Bio-logging technology

Since the beginnings of animal-attached remote sensing in the 1950s and 1960s (Eliassen, 1960, Arnold and Dewar, 2001), technological advancements in individual-based tracking technology (Ropert-Coudert and Wilson, 2005, Tomkiewicz et al., 2010) have shed light on the movements of a diverse range of species, including seabirds, while at-sea (Wilson et al., 2002, Burger and Shaffer, 2008). The development of Argos satellite-based tags, that can be monitored remotely through a central system (i.e. CLS, France) and provide accurate (~500 m) positional information (Hazel, 2009, Witt et al.,

2010) has removed the need to re-trap individuals to retrieve devices. The accuracy of these devices has been improved with the recent development of combined satellite and Global Positioning System (GPS) technology; Fastloc GPS-Argos tags record accurate (GPS) positional information and relay this through the Argos system (Sims et al., 2009, Witt et al., 2010). Nevertheless, battery life and device size is an issue (Phillips et al., 2003, Hart and Hyrenbach, 2009, Barron et al., 2010), confining early deployments to large species capable of being encumbered with devices (Jouventin and Weimerskirch, 1990).

In the last two decades, there have been two key developments in seabird bio-logging; the use of miniaturised global positioning system (GPS) loggers (Guilford et al., 2008), and the development of miniaturised light loggers capable of calculating coarse scale movements from light curves (geolocation)(Wilson et al., 1992, Afanasyev, 2004). Miniaturised GPS technology allows the logging of fine scale movements (< 20 m), and is ideal for monitoring foraging behaviour during the breeding season, but is confounded by battery life, memory storage, and the necessity of retrieving the device to access the data, making long-term deployments problematic. The use of geolocation devices can avoid some of these pitfalls as they require very little power or memory, and are small enough to attach to a leg ring. However, geographic positions calculated using light curves are typically only resolved to an error of circa 100-200 km (Phillips et al., 2004), and so this technology is unsuitable to study breeding season movements, or fine-scale foraging behaviour. Nevertheless, it is ideal for monitoring large-scale non-breeding movements and has become a popular tool for recording migratory and non-breeding behaviour over extended periods (Croxall et al., 2005, Phillips et al., 2005b, Egevang et al., 2010).

These technologies have linked individual movements with environmental variables (Louzao et al., 2010), and revealed how animals may target disparate prey patches across the marine environment (Weimerskirch, 2007). Prey can occur predictably within large-scale productive regions and a number of behavioural mechanisms revealed through bio-logging studies may allow individuals to target these areas (Sims et al., 2006, Tew Kai et al., 2009, Paiva et al., 2010a). Furthermore, the recent development of animal-borne miniaturised camera loggers may reveal how individuals assimilate fine-scale visual information to locate and capture prey (Watanuki et al., 2008, Sakamoto et al., 2009).

Information on dietary specialisation

Nevertheless, while GPS and geolocation loggers provide information on movement (Phillips et al., 2005b) and at-sea activity patterns (Mackley et al., 2010), they provide no information on diet. Instead, this can be gained through the collection and analysis of regurgitated prey items and pellets, the analysis of stomach contents, observations of courtship and chick feeding, or by targeting foraging aggregations (Votier et al., 2004a, Barrett et al., 2007). However, these techniques may be biased by temporal patterns in prey abundance and prey choice, or the quantity of indigestible material in prey (otoliths, squid beaks etc)(Votier et al., 2003), and it is not possible to link diet samples collected using these techniques with individuals during the non-breeding period (Furness et al., 2006, Barrett et al., 2007). Intrinsic biochemical markers, such as stable isotopes and fatty acids provide a useful complementary tool to conventional diet analysis (Bearhop et al., 2001, Käkelä et al., 2006). The ratios of stable carbon and nitrogen isotopes in consumer tissues reflect those of their prey in a predictable manner, for example individuals with higher nitrogen values generally feed on higher trophic level prey (Hobson et al., 1994, Inger and Bearhop, 2008). Tissues differ in their

metabolic activity, turn-over at different rates, and so integrate information on diet over different time scales. Therefore, by sampling tissues with known turn-over rates, diet can be reconstructed over a period of days (i.e. blood plasma), weeks (i.e. red blood cells, adipose tissue, muscle), months (i.e. feathers), or years (i.e. bone) (Marra et al., 1998, Hobson, 1999, Owen et al., 2010).

The importance of the annual cycle

Studies have linked dietary specialisation and breeding performance during the breeding season (Votier et al., 2004a), but we know little of the influence that migratory behaviour and winter food supply may have on individual condition and subsequent breeding performance (Daunt et al., 2006, Furness et al., 2006). Ecologists have long been aware that inter-seasonal effects may affect species abundance (Fretwell, 1972, Sutherland, 1996), and recent attention has been given to the theory that conditions experienced during one season may influence individual performance in the next (Harrison et al., 2010). It is important therefore to consider how individuals may respond to anthropogenic threats throughout the annual cycle. The combined application of bio-logging and stable isotope analysis can provide detailed information on the migratory movements, foraging behaviour and diet of individuals over multiple seasons and scales. By linking these with colony-based studies during the breeding season, it may be possible to document the potential consequences of different migratory and winter foraging strategies.

Predictive modelling techniques

Despite advances in tracking devices, bio-logging data is typically available for only a restricted number of species and locations. Not all breeding colonies are readily accessible, not all species are capable of carrying devices, and both devices and

deployments are costly. Furthermore, a consensus on the most appropriate method for data analysis is lacking (Wakefield et al., 2009). An alternative approach to examine the overlap between seabirds and anthropogenic threats would be to collate information from colony-based counts and model at-sea distributions based on known foraging ranges (BirdLife, 2010b). This technique may lack the rigour of bio-logging studies, but is inexpensive, quick to implement and could be used across a wide-range of species and groups. It also provides a method to highlight the potential for interactions between anthropogenic activities at-sea, and seabirds from known colonies.

Study species

The purpose of this project was to quantify the interactions between seabird populations in the south west of England and the proposed site of a new Marine Renewable Energy Installation (MREI), the Wave Hub, situated off the northern coast of Cornwall.
The south west of the UK is home to a number of important seabird colonies, and this thesis focuses on two species of interest (Figure 1.1).

The northern gannet *Morus bassanus* (hereafter gannet) is a large (circa 3 kg) well studied apex marine predator, and the only member of the genus *Morus* to breed in the Northern hemisphere, at colonies across the North Atlantic, from Newfoundland to Norway, and from France to Iceland (Lewis et al., 2001, Nelson, 2002, Grémillet et al., 2006, Wanless et al., 2006, Hamer et al., 2009). Bio-logging studies have revealed a number of over-wintering areas, including the North Sea, Bay of Biscay, Mediterranean, and Northwest African coast (Kubetzki et al., 2009). Approximately, 40,000 pairs of gannets breed on Grassholm Island, Pembrokeshire (51.730°N, 5.486°W) and forage across the Celtic Sea and north Cornish coast (Votier et al., 2010). The gannet is a wide-ranging plunge-diving generalist piscivore, and is also known to target fisheries discards

facultatively (Votier et al., 2010). Studies of gannets have documented foraging trips ranging from tens to hundreds of kilometres in length (Hamer et al., 2001) and so gannets could be impacted by threats many kilometres from the colony. However, at the population level, this wide-ranging and flexible foraging behaviour could also mitigate anthropogenic threats.

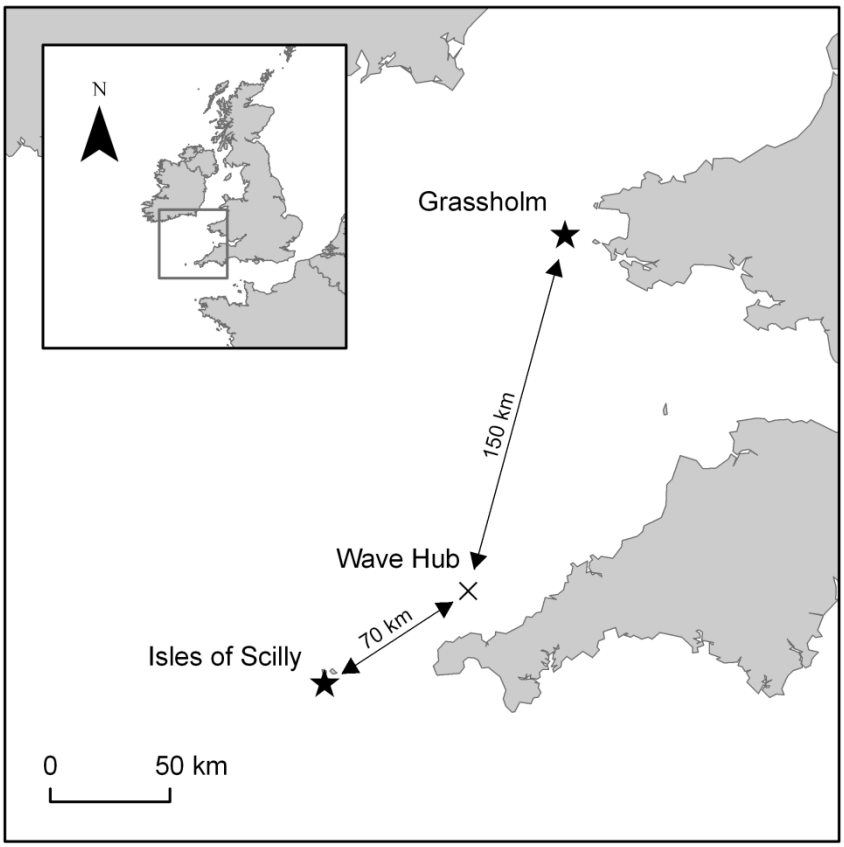

Figure 1.1 Location of focal seabird colonies in relation to the Wave Hub development site. Both Northern gannets *Morus bassanus* breeding on Grassholm Island and lesser black-backed gulls *Larus fuscus* breeding on the Isles of Scilly are capable of foraging within the Wave Hub site.

The second species of interest is the lesser black-backed gull *Larus fuscus*. Populations in the UK have seen a number of changes in recent years, with colonies in rural areas experiencing precipitous declines while populations in urban areas have been on a steady increase since the 1970s. The UK holds around 70% of the global population of

the *graellsii* sub-species of the lesser black-backed gull *Larus fuscus graellsii* (Wernham et al., 2002) and the stronghold for this sub-species is in the southwest of the UK. Gaining a better understanding of what is driving this change is therefore paramount to UK conservation efforts. Lesser black-backed gulls are a mid-sized gull species (circa 800 g) and traditionally oceanic foragers although, like many other gull species, they will also target anthropogenic waste, and are capable of foraging over 100 km from colonies during the breeding season (Camphuysen, 1995). This places the Wave Hub site well within the foraging range of a number of colonies in south-west England, including the large colonies on the Isles of Scilly.

Therefore, I selected these two species because they are (1) large enough to carry bio-logging devices, (2) capable of foraging within the range of the proposed Wave Hub site, and (3) breed at readily accessible colonies.

1.2 AIMS OF THE THESIS

In **Chapter 2** I describe the range of wave-powered energy generating devices currently either operational or in development in the UK, and review the potential threats and benefits of these to marine birds, their habitats and prey. Recent studies have been critical of the methods used in the assessment of wind-powered MREI impacts, and I suggest solutions for the design of future studies into the effects of MREIs.

In **Chapter 3** I develop a technique to identify important areas for breeding seabirds based on at-sea projections from colonies. I synthesise data from colony surveys with detailed information on population dynamics, foraging ecology and near-colony behaviour, to project colony-specific foraging distributions of gannets breeding at colonies in the UK, Ireland and France.

In **Chapter 4** I combine two approaches to describe the migration strategies of gannets from two breeding colonies in the north-west Atlantic: geolocation sensors (GLS) to track individuals over multiple seasons, and the analysis of stable isotope ratios in consumer tissues to provide information on dietary preferences during the wintering period. I investigate the role of migratory fidelity and potential carry-over effects of particular wintering strategies.

I go on to further this work in **Chapter 5** by considering the movements of four seabird species and one sea turtle species known to utilise the Northwest African upwelling region during the non-breeding period. This area is a known biodiversity hotspot but has recently been under increased fishing pressure. I compare the distribution of individuals tracked through the non-breeding period with environmental variables and contemporaneous fishing data, then examine historical trends in the recovery of marked individuals and fishing effort in the region. A network of pelagic MPAs are required to alleviate anthropogenic threats on the marine environment, and the Northwest upwelling region provides a suitable candidate.

In **Chapter 6** I bring together the various threads that I have explored in my thesis, I consider some of the problems that arose during the project and discuss the main findings of each chapter in a broader context.

Chapter 2:
Potential impacts of wave-powered marine renewable energy installations on marine birds

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ABSTRACT

One likely method of combating the potential impacts of climate change is the expansion of renewable energy installations, potentially leading to an increase in the number of wave-powered Marine Renewable Energy Installations (MREIs). The consequences of increased use of these devices for birds are unknown. Here we describe the wave-powered energy generating devices currently either operational or in development and review the potential threats and benefits of these to marine birds, their habitats and prey. Direct negative effects include risk of collision, disturbance, displacement and redirection of migrating birds during construction, operation and decommissioning. Above-water collision is a particular concern with wind-powered devices, but, because of their low profiles, the collision risk associated with wave-powered devices is likely to be much less. Conversely, wave devices also pose the novel threat of underwater collision. Wave-energy generating devices may indirectly impact marine birds by altering oceanographic processes and food availability, with implications for trophic cascades. Through appropriate mitigation, wave-powered MREIs offer the potential to enhance habitats. Direct positive effects may include

provision of roosting sites, and indirect positive effects may include prey colonisation through the provision of suitable substrates for sessile organisms, the attraction of fish to MREIs acting as Fish Aggregating Devices (FADs), or because they act as *de facto* protected areas. The cumulative effect of these could be the improvement and protection of foraging opportunities for marine birds. Recent studies have been critical of the methods used in the assessment of wind-powered MREI impacts, which lack sufficient sample sizes, controls or pre-development comparisons. Here we suggest solutions for the design of future studies into the effects of MREIs. Wave-powered MREIs are certain to become part of the marine environment; but, with appropriate planning, mitigation, and monitoring they have the potential to offer benefits to marine birds in the future.

2.1 INTRODUCTION

It is widely accepted that a significant proportion of increasing greenhouse gas emissions are derived from anthropogenic sources, and while the consequences of such global change are under debate, the evidence indicates that environmental change can have global scale impacts on avian biodiversity, population dynamics and phenology (IPCC, 2001, Pounds and Puschendorf, 2004, Thomas et al., 2004, Huntley et al., 2006).

Marine Renewable Energy Installations (MREIs) offer the prospect of generating clean, low carbon energy without the problems associated with finding suitable sites on land (Taylor, 2004, Fox et al., 2006, Oxley, 2006, Markard and Petersen, 2009), providing a solution to reducing the current dependence on fossil fuels and a method of meeting national targets for sustainable development. The UK has large offshore wind and wave resources and, in line with other EU member states, has seen a rapid increase in the number of energy generating devices, predominantly wind-powered, on and around its shores (Gill and Kimber, 2005, Desholm et al., 2006). However, further expansion of the renewables sector will require diversification to prevent reliance on any one technology.

Wave energy is a promising new method for marine powered energy generation, representing a widely obtainable and consistent energy source with a potentially low environmental impact, although this is yet to be quantified (Leijon et al., 2003, Henfridsson et al., 2007). New MREIs will be positioned to maximise potential energy return; shallow areas of ocean that experience either high annual wind speeds for utilisation by wind-powered MREIs, or regular large swell or tidal current races for, respectively, wave- and tidal-powered MREIs. These neritic (the area of ocean between the low-tide mark and continental shelf) areas are important habitats for a number of

taxa, and any potentially negative impacts of MREIs need to be mitigated, avoided, or lost habitat provided for elsewhere. To date, few data have been collected offshore due to the expense of at-sea surveys (Desholm and Kahlert, 2005), leaving a lack of information on habitat utilisation of potential development areas by marine birds.

Although many taxa may be impacted by MREI development, marine birds (seabirds, sea ducks, divers and grebes) are one of the most easily studied because they are relatively abundant, conspicuous, and occur above water. Also, as apex predators, they integrate conditions over broad spatio-temporal scales, and are often used as convenient models for studying the effects of environmental change (Furness and Camphuysen, 1997). To date, work has focused on how changes in extrinsic factors such as fisheries (Frederiksen et al., 2004, Votier et al., 2004b, Phillips et al., 2006, Votier et al., 2010), climate (Votier et al., 2005, Frederiksen et al., 2007a, Rolland et al., 2008, Grémillet and Boulinier, 2009), and pollution (Votier et al., 2005, Altwegg et al., 2008, Votier et al., 2008b) can shape marine bird behaviour, foraging, movements, and population dynamics, but few investigate the implications of offshore development.

The ecological impacts of the expanding offshore wind industry have been the focus of much research (Desholm and Kahlert, 2005, Chamberlain et al., 2006, Desholm et al., 2006, Dierschke et al., 2006, Drewitt and Langston, 2006, Huppop et al., 2006, Masden et al., 2009), although the impact of offshore windfarms on the population dynamics of birds remains unclear (Stewart et al., 2007). However, there are few data on the environmental impacts of offshore wave or tidal energies on biodiversity (but see Langhamer et al., 2010). Here we discuss the potential impacts of wave-powered MREIs on marine birds. Due to the lack of studies it is not possible to conduct a conventional review, instead we describe the range of devices currently operational or

under development, discuss how they might affect marine birds directly, or indirectly via their prey and habitats, and then consider possible population-level impacts, using evidence from wind-powered MREIs when wave-powered examples are unavailable. Moreover, we answer some methodological criticisms of ecological impact monitoring at MREI sites in general, and wave-powered devices in particular, with suggestions for appropriate experimental design.

2.2 WAVE ENERGY CONVERTERS

Wave-powered MREIs differ widely from wind turbines (Figure 2.1a) and will use a variety of technologies and methods to harness wave energy, with a range of possible impacts on marine birds, their habitats and prey. We first introduce the range of methods, giving key examples of the wave devices currently in development or operational.

1) Point Absorbers

A point absorber is a floating device that sits on the surface and absorbs energy in all directions as it moves with the waves. There are a number of different power take-off methods to convert this motion into useful energy, but one method is to convert the directional movement into a stroking motion which in turn will drive a hydraulic ram. Examples of point absorbers include the PowerBuoy device from Ocean Power Technologies (www.oceanpowertechnologies.com), and the Fred Olsen Buldra/ FO^3 concept (www.seewec.org) (Figure 2.1b-c).

2) Attenuators

These devices either sit high in the water column, or float on the surface, operating perpendicular to the wave direction. Wave movements are transported down the length

of the device as it rides the waves. Devices can be articulated, as in the case of Pelamis, (Figure 2.1d) currently being developed by Pelamis Wave Power Ltd (www.pelamiswave.com). This uses hydraulic rams positioned between the articulations, and compressed by the movement of the device, to generate electricity.

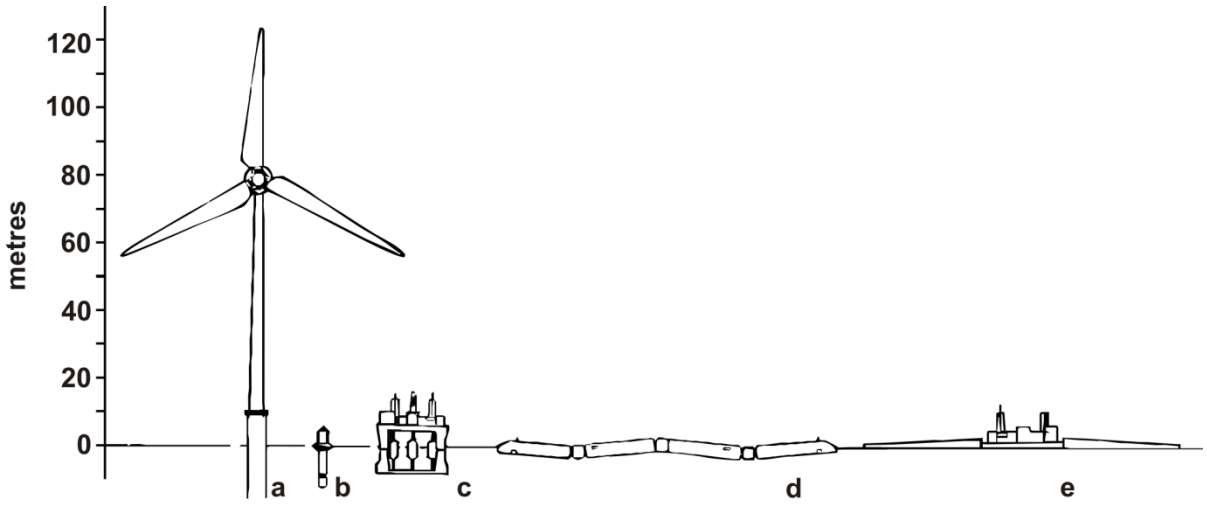

Figure 2.1 Wind turbines **(a)** offer a much more significant collision risk due to their height and extended sweep of the rotors. Wave-powered MREIs such as **b)** the OPT Powerbuoy, **c)** Fred Olsen Buldra, **d)** Pelamis, and **e)** Wave Dragon present a much smaller collision risk to seabirds by being semi-submerged and offering a reduced profile.

3) Overtopping Devices

These use a floating reservoir that collects water from waves as they break over the device. This water is held in the reservoir and then returned to the sea through low-head turbines thus generating electricity, much like existing hydroelectric systems. The Wave Dragon, constructed by Wave Dragon ApS (www.wavedragon.net) is such a device (Figure 2.1e).

4) Submerged Pressure Differential

These devices operate in a similar manner to point absorbers, but are fully submerged. Wave motion forces the device up and down, creating a pressure differential which can

be used to pump hydraulics and generate electricity. AWS Ocean Energy (www.awsocean.com) are currently designing the AWS-III/ Archimedes Wave Swing (Figure 2.2a).

5) Oscillating Wave Surge Converters

These use a pendulum that sits in the water column, as the wave surge passes, the pendulum oscillates on a pivot, which in turn drives hydraulic pistons. A commercial scale example is the Oyster device, developed by Aquamarine Power Ltd (www.aquamarinepower.com) (Figure 2.2b).

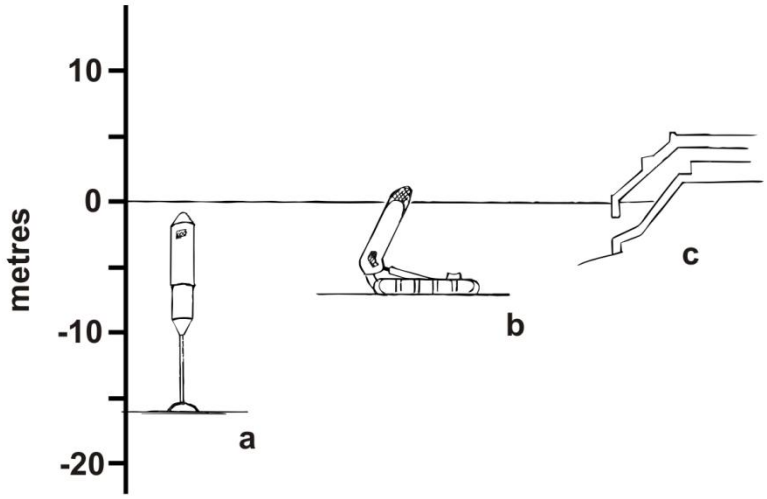

Figure 2.2 Wave-powered MREIs will be highly mobile underwater i.e. **a)** Archimedes Wave Swing, **b)** Oyster, pose the novel threat of underwater collision, or will contain chambers that may trap marine birds, i.e. **c)** Limpet.

6) Oscillating Water Column (OWC)

Typically, OWC devices are semi-submerged in the water column, encapsulating a pocket of air in a chamber while being open to the sea below. Waves cause the water level to rise and fall, compressing the air and forcing it through a turbine. This

technology has been successfully deployed by Hydro Wavegen Ltd. (www.wavegen.co.uk), and a Limpit device has been installed on Islay, Inner Hebrides, Scotland (Figure 2.2c).

2.3 POTENTIAL NEGATIVE INTERACTIONS WITH MARINE BIRDS

Risk of collision above water

It is well established that the greatest threat of wind-turbines to birds is the risk of collision (Huppop et al., 2006, Montevecchi, 2006). However, because wave-powered devices have a much smaller profile, they may represent a much lower collision risk. For example, Attenuators, Point Absorbers and other buoy-like wave-powered MREIs are unlikely to extrude more than 4 m from the water surface (Michel et al., 2007), in contrast to wind turbines which may be over 120m tall (Figure 2.1). However, not all devices will have a small footprint and unlike wind turbines, will contain mobile components both on and below the water surface, with consequences for birds in flight and whilst diving.

The existing literature on wind-turbine impacts has shown avoidance ability and vulnerability to collision to vary as a function of species and size (Brown et al., 1992, Garthe and Huppop, 2004, Lucas et al., 2008), and nocturnal or crepuscular species may be more affected by being active during periods of low light (Larsen and Guillemette, 2007, Arnett et al., 2008). Furthermore, age and reproductive stage may affect collision risk (Henderson et al., 1996), and differential mortality between age classes would affect population dynamics (Votier et al., 2008b). These differences in collision risk may also apply to the, albeit low, risk of collision with wave-powered devices.

Even so, few studies have quantified how collision risk might vary with environmental conditions, particularly during bad weather when marine birds would be at greater risk due to reduced visibility and manoeuvrability. Further work is required to quantify the potential collision risks posed by these devices, and how risk may vary between species and environmental conditions, allowing mitigation of any effect to be incorporated at an early stage in the process.

Risk of collision under water

Wave-powered MREIs represent an underwater collision risk to diving birds. Fixed structures under the surface pose little risk due to their ease of navigation; however the devices, anchor chains and cabling will be highly mobile and so harder to navigate (Wilson et al., 2007) (Figure 2.2). No work to date has quantified the potential collision risks to marine birds associated with wave-powered MREIs, although Tidal Energy Converter (TEC) turbines have low rotational speeds (*circa* 15 rpm) and are unlikely to cause injury during a collision event (Fraenkel, 2006). Risk will be highest when marine birds are diving for prey, and so sensitivity will depend on the ecology of the species, with the highest potential for interaction occurring when a device is placed within the foraging range of a colony and at a depth within the dive profile. It is paramount therefore to understand the distribution and behaviour of prey species in response to these devices, to allow a better understanding of the potential conflicts between marine birds and wave-powered MREIs.

Sensitivity will also vary as a function of avoidance ability: surface divers have typically slow and controlled dive profiles, while plunge diving species have lower margin for avoidance and so may be more threatened (Ropert-Coudert et al., 2004, Thaxter et al., 2009). Turbidity will increase around the moving parts of a wave-

powered MREI (Langhamer et al., 2009), thus reducing visibility and increasing the potential collision risk. While diving behaviour has been linked to both visibility (Haney and Stone, 1988, Henkel, 2006) and tide (Holm and Burger, 2009), no work to date has investigated the collision risk associated with underwater structures, although attempts have been made to quantify mortality around offshore oil platforms which present a collision and pollution risk (Wiese et al., 2001).

Risk of entrapment

Devices that use pressure differentials to drive internal turbines, such as oscillating water columns (Figure 2.2c), or overtopping devices (Figure 2.1c) will contain enclosed chamber sections that are partially exposed to the open ocean. These openings pose a risk of entrapment to marine birds that are capable of entering the chamber and could be killed either by the turbines, or by the propulsion of water from within the device. These risks would differ between the device and installation type, but could be mitigated simply by covering openings with a protective mesh.

Disturbance

Any impact of operational noise will be most significant during installation of the devices, and subsequent maintenance activities (Madsen et al., 2006). Devices capable of floating rather than being fixed in the seabed would minimise the impact of noise during construction by negating the need for pile driving, an activity that has the potential to cause auditory damage to wildlife in the vicinity (Thomsen et al., 2006 , Snyder and Kaiser, 2009). Nevertheless, wave-powered MREIs will require the construction of extensive moorings and anchorage to maintain efficient operation. Natural wariness to anthropogenic activity might exclude animals from the critical area

during construction thus reducing the potential impact (Burger, 1988, Koschinski et al., 2003), but responses vary with the stimuli and are hard to quantify (Hill et al., 1997).

A wide range of operational noise will be produced by the equipment and associated anchorage and cabling; the potential impacts of these are unknown and there are no studies currently quantifying wave-powered MREI noise, or the impacts on marine birds. Studies suggest the noise produced by wind turbines may mask biologically significant sounds or even damage acoustic systems in a range of species (Southall et al., 2000, Gill and Kimber, 2005), although there is evidence of habituation after construction in geese (Madsen and Boertmann, 2008) and marine mammals (Madsen et al., 2006). Further work should focus on understanding the baseline soundscape in these environments before development to allow a comparison with noise levels after installation, as has been done in urban environments (Habib et al., 2007).

Displacement

The area of seabed directly impacted during the construction of wave-powered MREIs will be small, limited to impacts from cabling and anchorage (Langhamer and Wilhelmsson, 2009). Nevertheless, some devices, such as oscillating wave converters will require a fixed base. This is similar to the impacts suggested during wind turbine construction; however, the construction and decommissioning of the devices themselves differs substantially and loss of habitat throughout these phases is likely to be less extensive (reviewed by Gill, 2005).

Disturbance and removal of habitat may lead to displacement of animals from the vicinity of the development site. Displacement will take two forms: (1) birds may avoid areas containing man-made structures (Petersen et al., 2006, Larsen and Guillemette,

2007), or (2) foundations and associated cabling around MREIs may alter hydrological process and make the environment unsuitable for prey species (Kaiser et al., 2006b).

For marine birds that forage in shallow sandy areas suitable for MREIs, displacement could have a disproportionately negative impact (Snyder and Kaiser, 2009). However, wave-powered MREIs, which either float on the water surface, or are stable in the water column and are anchored to the seabed, are likely to have less of an impact than pile driven turbines (Mueller and Wallace, 2008, Inger et al., 2009). Furthermore, impacts during construction are time-bound; in contrast fishing activities such as trawling are repetitive leading to cumulative impacts on the benthos as the habitat is not allowed to recover (Kaiser et al., 2006a).

Redirection

Developments have the potential to form extensive barriers to movement (Gill, 2005), and marine birds may be forced to navigate around wave-powered MREIs in the same way that they avoid wind-powered MREI, increasing both distance travelled and energy expenditure (Desholm, 2003, Masden et al., 2009). However, the energetic requirements of wind farm avoidance are limited unless repeated regularly; navigating around a medium sized wind farm extended the migration distance of common eider *Somateria mollissima* by ca 500 m (0.04%) at a negligible cost to body condition. To achieve a loss in body mass in excess of 1% this response would need to be repeated 100 times (increasing the migration distance by 4%) (Masden et al., 2009). Therefore, it is unlikely that multiple wind-powered MREIs sites will impact migration routes, and for wave-powered MREIs with inherently low profiles the impact will be negligible. Nevertheless, not all devices have a low profile; commercial scale developments such as the Fred Olsen Buldra/ FO^3 concept (www.seewec.org) (Figure 2.1c) house a number of

point absorbers in a more traditional offshore rig that will be 24 m high. Work is required to investigate the re-directional effect of devices with differing heights.

Furthermore, many marine bird species have altricial young and so are confined to central placed foraging during the breeding season. Conflict may arise if installations were sited between feeding, breeding and roosting grounds, and navigated frequently (Langston and Pullan, 2003, Desholm and Kahlert, 2005, Masden et al., 2010b). Changes in energy balance may affect fitness, but need to be placed in context with the wider energetic pressures on a population (Masden et al., 2010b).

Pollution

Wave-powered MREI devices will contain substantial amounts of oil and lubricant for effective operation at sea, which carries a spill potential. There is currently no evidence to determine how frequently this occurs or whether it would have any impact, but major oil pollution events are known to have wide-scale population-level consequences for marine birds (Votier et al., 2005, Votier et al., 2008b).

2.4 POTENTIAL POSITIVE INTERACTIONS WITH MARINE BIRDS

Roosting

The construction of new structures in the marine environment creates roosting sites that are quickly used by marine birds, as found around oil platforms (Wiese et al., 2001). If wave-powered MREIs were to act as roosting sites they could potentially increase foraging ranges of certain species, or provide resting sites for migratory terrestrial birds normally unable to land on the water. However, manufacturers are likely to deliberately design buoys to deter roosting since prolonged use may cause damage and reduce

device efficiency (Michel et al., 2007), and aggregation around a device is likely to increase collision risk.

2.5 POTENTIAL NEGATIVE INTERACTIONS WITH HABITATS AND PREY

It is harder to elucidate the indirect impacts that wave-powered MREIs may have on local habitats and prey species, but these could be of equal importance to marine birds, leading to population level changes.

Changes to oceanographic processes

There is the potential for wave-powered MREIs to reduce foraging opportunities for birds through trophic changes resulting from altered oceanographic processes (Frederiksen et al., 2007b). Attenuators such as Pelamis may extract up to 23% of the incidental energy from a wave (Palha et al., 2010), although the efficiency of energy extraction will differ between devices and wave states. The area of ocean affected by the wave shadow produced by an array will also move relative to the prevailing wave and wind direction (Millar et al., 2007). A reduction in wave energy could impact transport processes (Pelc and Fujita, 2002) and could be detrimental to spawning or nursery sites (Gill, 2005). Conversely, reducing the ability of currents to move sediment would lead to the accumulation of organic matter, increasing biodiversity by providing habitat for deposit and suspension feeders such as polychaetes (Fabi et al., 2002). In coastal sites there is also the potential for a scale-dependent reduction in the wave energy that reaches the shore, which could lead to changes in sedimentation and shoreline processes (Millar et al., 2007).

The potential bottom-up effects of these impacts and their scale are unknown, but if predicted changes to the micro-scale tidal climate within an MREI were to have a

detrimental impact on spawning and larval recruitment in the surrounding area (Gill, 2005), the likely outcome would be a reduction in food availability for higher trophic level animals such as birds. Further work is required to quantify both the wave shadow produced by large arrays of devices, and the environmental consequences.

Changes to food availability

Foraging opportunities for birds could be altered through detrimental changes to local scale habitat around wave-powered MREIs, although there may also be beneficial effects through enhancement of small-scale hydrographic processes such as eddies. Novel structures placed in areas with little or no hard substrate will enable the colonisation of sandy areas by hard-bottom dwelling species (Bulleri et al., 2003). Studies on the colonisation of wind-powered MREI show them to be dominated by blue mussels *Mytilus trossulus* and acorn barnacles *Balanus improvisus*, with altered fish communities containing higher abundance but lower species diversity (Wilhelmsson et al., 2006). Invasive species typically colonise more rapidly than indigenous species following disturbance (Bulleri and Airoldi, 2005), which could impact marine birds if invasive species out-competed preferred prey species, but could also offer benefits if the monocultures were exploited (see positive interactions below).

The installation of tidal turbines in the Bay of Fundy has been demonstrated to increase the mortality of migratory fish populations, with potential consequences for the marine animals reliant on this seasonal resource (Dadswell and Rulifson, 1994). The redirection of fish migration routes away from areas with large arrays would have obvious deleterious effects for piscivorous bird species. An increase in fish mortality due to collision or entrapment would have a long-term negative effect, although there may be short-term benefits for scavenging species.

2.6 POTENTIAL POSITIVE INTERACTIONS WITH HABITATS AND PREY

Habitat enhancement

Wave-powered MREIs could attract marine organisms through the addition of hard substrate to the ecosystem and formation of artificial reefs (Baine, 2001, Whitmarsh et al., 2008). Wave- and wind-powered MREIs have been shown to provide anchorage for a number of sessile species such as blue mussels and acorn barnacles (Sundberg and Langhamer, 2005, Wilhelmsson and Malm, 2008, Langhamer et al., 2009). This offers potential benefits to shellfish eating species such as common eider that could capitalise on the increased food resource. Nevertheless, invasive species are quick to colonise new habitats and may outcompete native prey species (Fridley et al., 2007), but due to the complex nature of trophic linkages (Anthony et al., 2008) the effects of such change could be very difficult to predict.

Colonisation will cause conflict if it interferes with equipment performance (Michel et al., 2007), and experimental studies estimate the level of biofouling may be as high as 150 kg of biomass per 3 m diameter buoy (Langhamer et al., 2010), but scouring to enhance efficiency may not be cost effective (Langhamer et al., 2009).

Aggregation

Floating wave-powered MREIs could act as fish aggregation devices (FADs), attracting and recruiting fish species seeking protection and food (Hunter and Mitchell, 1968, Nelson, 2003, Sundberg and Langhamer, 2005). Wind turbine monopiles have been shown to act as both artificial reefs and FADs as they are positioned vertically in the water column, increasing the density of fish within the vicinity; although there may be consequences for community structure, species richness and diversity (Wilhelmsson et al., 2006). Both species richness and assemblage size are positively correlated with

FAD size (Nelson, 2003), so large wave-powered MREI will be better at recruiting fish species, thus providing foraging opportunities for piscivorous birds.

De facto MPA designation

Navigational aids and buffer zones will be installed around the MREI to limit boat traffic and prevent either fouling of the machinery by fishing gear, or vessel collisions. Larger installations with a number of devices, especially wave and tidal energy converters, will have enforced closures and 500 m exclusion zones to protect the deployed equipment (SWRDA, 2006), and it is unlikely that fishing vessels will enter the array due to the risks of entanglement. Indeed current regulations will exclude commercial fishing from development sites, providing refugia from fishing (Gill and Kimber, 2005) but the response of local stakeholders is unknown. No-take zones are increasingly being promoted by fisheries managers, policy makers, conservationists and ecologists to reduce the overexploitation of fish stocks (Sanchirico et al., 2006).

This potential for protection, combined with the provision of novel hard substrate by device installation could increase biodiversity, as lower trophic species recruit to colonise the new habitat, offering an aggregated and effectively protected resource for marine birds. As a result MREIs may act as *de facto* marine protected areas (MPAs) (Sundberg and Langhamer, 2005, Inger et al., 2009), with potential benefits for marine birds. However, any potential benefit to local-scale fish abundance could lead to "fishing the line" (Kellner et al., 2007, Stobart et al., 2009), by attracting fisheries to the edges of the exclusion zone due to spill over effects.

2.7 POPULATION-LEVEL AND SYNERGISTIC EFFECTS

Trophic cascades have been shown to affect seabird populations by altering food supplies in complex ways (Österblom et al., 2006, Frederiksen et al., 2007b). Therefore as well as the effects of changes in food availability mentioned above, there may be unforeseen community level changes in trophic interactions, although the magnitude of any effect will determine to what extent these might have consequences at the population-level (Elphick, 2008). It is also unclear how the ecosystem will respond to such perturbation, and further work is required to investigate how the potential positive and negative effects may offset one another.

While mortality due to collision will affect only a small proportion of the population (Lucas et al., 2008, Desholm, 2009), there is the potential for cumulative indirect effects to affect the entire population; for example through extended reduction in body condition of all breeding adults through the insensitive placement of multiple installations on a migration flyway (Masden et al., 2009). The potential for cumulative negative impacts could potentially constrain development of multiple wave-powered MREIs, and consideration would be required through both Environmental Impact Assessment (EIA), and Strategic Environmental Assessment (SEA) (Devereux et al., 2008, Masden et al., 2010a).

2.8 PROSPECTUS FOR FUTURE RESEARCH

The existing data on potential impacts of wind-powered MREIs is expansive, but inadequate experimental designs make comparisons problematic (Stewart et al., 2007). Gaining a better understanding of impacts requires further meta-analyses, but crucially these require common methodologies. Due to the slow development of other types of MREI, information on the impacts of wave- and tidal-powered MREIs is poor, and the

available information on wind farms does not translate well to wave-powered technologies. However, appreciating the errors made during the study of wind farms is critical in preventing the same mistakes being made in the development of studies into wave-powered MREI effects. It is vital to involve stakeholders through the process of developing and managing an MREI site. In this way the science can be built in from the start, allowing for appropriate monitoring programs to be managed throughout the lifespan of an MREI.

More data are required to elucidate the causes of observed changes in fauna around existing MREIs and to predict the potential effects of future developments. Stewart *et al.* (2007) and Langston *et al.* (2006) call for better standards of EIA and post-construction monitoring, as much of the reviewed work in Stewart *et al.* (2007) did not include either controls or pre-development comparisons, but this is now being addressed (Pearce-Higgins et al., 2009, Masden et al., 2010a). Studies that focus on one site, with no control for a comparison, lack the power of more complex studies. The use of Before-After-Control Impact (BACI) assessment (Underwood, 1992) over an appropriate timescale, with a minimum monitoring period of 1 year before impact to ensure monitoring of any annual cycles in species, and monitoring of the construction area over 5-10 years for any long-term post-construction effects (Langston and Pullan, 2003), should be the minimum standard in future research studies of MREI impacts.

Stewart *et al.* (2005) call for BACI designs to incorporate replicated and balanced experimental designs with randomised sampling regimes. Future developments need to incorporate well-designed and replicated monitoring from the initial planning stages through to completion. This should be followed by long-term monitoring of the site in order to look at both immediate and temporal changes over appropriate timescales. In

combination, this will enable robust examination of changes at the individual site level, as well as providing the criteria for multi-development level comparisons.

Theoretical considerations

Marine birds are highly K-selected, exhibiting low birth rates and prolonged development, and so are sensitive to changes in adult survival (Sæther and Bakke, 2000). The majority of mortality occurs during the inter-breeding period (Barbraud and Weimerskirch, 2003), but the impacts of wave-powered MREI during the non-breeding season are currently unknown. Furthermore, many current seabird declines are attributed to reproductive failure due to low food availability (e.g. Frederiksen et al., 2007b). Future studies should focus on understanding the potential for wave-powered MREI to increase adult mortality or alter food supplies during the breeding season, but teasing apart the effects of MREIs over and above other factors is not straightforward.

A population level response is ultimately determined by individual level choices, ranging from disturbance, migration, and predation, to habitat patch utilisation (Sutherland, 1996, Inger et al., 2006). Only through understanding the individual level responses to MREIs can the population level effects be elucidated. This will require individual based studies (e.g. mark/recapture and animal tracking) to identify the survival for whole, and sub-sections, of populations, and demographic studies to understand sensitivities to mortality (Desholm, 2009). Marine bird populations contain large non-breeding components, which can buffer changes in population size due to temporary increases in adult mortality (Votier et al., 2008b); however due to the ephemeral nature of this age class little is understood of their movements away from the colony.

During the breeding season most seabirds act as centrally placed foragers and are restricted in the foraging habitat they can exploit. Therefore, an important question is to link breeding colonies with specific foraging areas before being able to mitigate the potential effects of building MREIs in these areas. If MREIs were to act as FADs/MPAs then they could offer benefits to colonies if placed strategically. However, marine birds also have different breeding and wintering ranges, which would require consideration at the planning stage.

Practical considerations

There is a clear need for the integration of multi-disciplinary scientific research, necessitating the use of a number of techniques to expand on the potential impacts of MREIs on seabird populations. In addition to BACI standardised survey methodology, gaining a detailed understanding of seabird movements and habitat utilisation would allow the mitigation of potential conflicts with offshore site designation and device operators.

Wave-powered MREI technology is still in its infancy, and to date there are only a limited number of active sites in the UK and Ireland. As technology develops, consideration of the spatial distribution of sites will help mitigate any cumulative device impact while maximising the potential benefits. Figure 2.3 illustrates the potential overlap between seabirds (from Mitchell et al., 2004) and currently planned or operating MREIs: the Round 3 Offshore Wind Development Zones; the European Marine Energy Centre (EMEC) in Orkney, Scotland (www.emec.org.uk/); the site of SeaGen in Strangford Lough, Northern Ireland (www.seageneration.co.uk/); and Wave Hub, Cornwall, UK (www.wavehub.co.uk/), the latter appearing to have the lowest potential overlap. To understand the use of these areas by seabirds, as well as other marine birds,

will require the integration of land-based surveys to pin-point colonies potentially impacted by developments, with tracking studies to understand movements from those colonies. In the UK, the establishment of the Seabird Monitoring Programme and its outputs (e.g. Mitchell et al., 2004) provide these data, which could then be used to model hotspots of activity, and in turn provide comparisons with existing at-sea surveys.

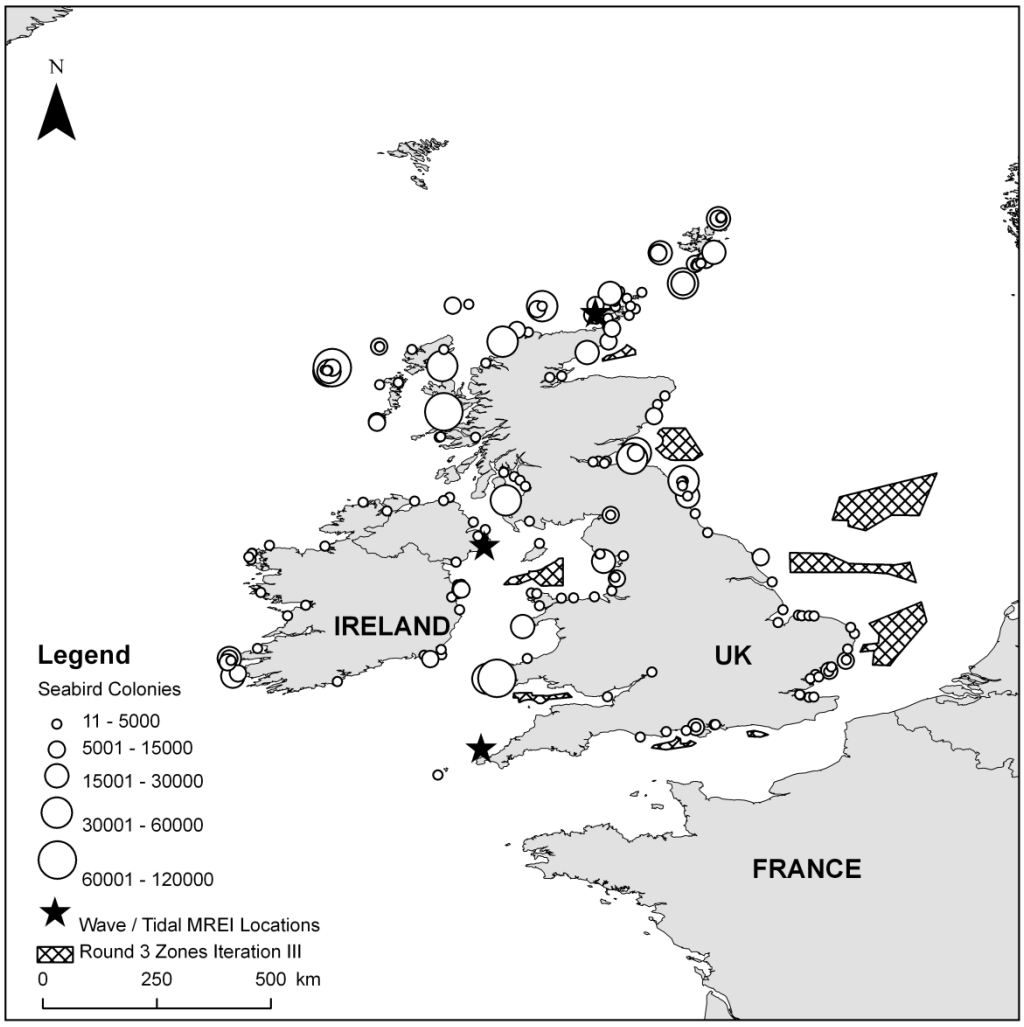

Figure 2.3 Spatial overlap between key seabird colonies and MREI installations in the UK and Ireland. Locations are shown for colonies containing at least 1% of the UK and Irish breeding population for a species, scaled to represent population size. Extant wave and tidal MREI locations are Wave Hub (St Ives, Cornwall), SeaGen (Strangford Lough, Ireland) and EMEC (Orkney, Scotland). Wind-powered MREIs are represented by The Crown Estate Round 3 designations for offshore wind farm development.

Experimental design

The lack of available data and the minimal number of devices currently operational on a global scale highlights the need for robust survey methods optimised to detect ecologically significant changes in bird species abundance and distribution, should they occur. Critically, early adoption of broad scale standardised methods would allow the involvement of science in the design and installation of future MREI sites. One study currently underway looks at the biodiversity impacts of the Wave Hub project (www.primare.org), the UK's first large-scale offshore test facility for wave energy conversion devices. To refine the experimental design for monitoring potential impacts on marine birds, we undertook a prospective power analysis after completing five at-sea surveys at the proposed Wave Hub site. This allowed us to gain a better understanding of the variability of seabird numbers at the site, thus enabling the determination of an appropriate number of replicates with which to detect any future statistically significant changes in abundance.

Power typically represents the probability of rejecting a false null hypothesis (Gerrodette, 1987), and power analysis provides a useful tool in the planning phase of ecological experiments and the interpretation of non-significant results (Di Stefano, 2003). We constructed a power analysis in R 2.6.2 (R Development Core Team 2008) to evaluate the effect of sample size and effect size on power, demonstrating how increases in sample size change the ability to detect a signal. The test was a comparison of the mean bird abundance between two groups: control (point counts of bird abundance outside the Wave Hub site) and experimental (point counts of bird abundance within the Wave Hub development), with varying numbers of replicates within the groups. The experimental effect was a percentage reduction in the mean number of birds within a replicate (Figure 2.4). Replication is vital in order to detect

potential impacts as power increases with replication: for moderate effect sizes small increases in the sample sizes would have larger implications for the power of the study. However, if the effect size signal is very small then there is little chance of detection even with relatively large numbers of treatments. For a power of 80% and a minimum of ten replicates per treatment, our analysis would suggest a statistically significant reduction in the mean abundance of marine birds by 35% would be detectable.

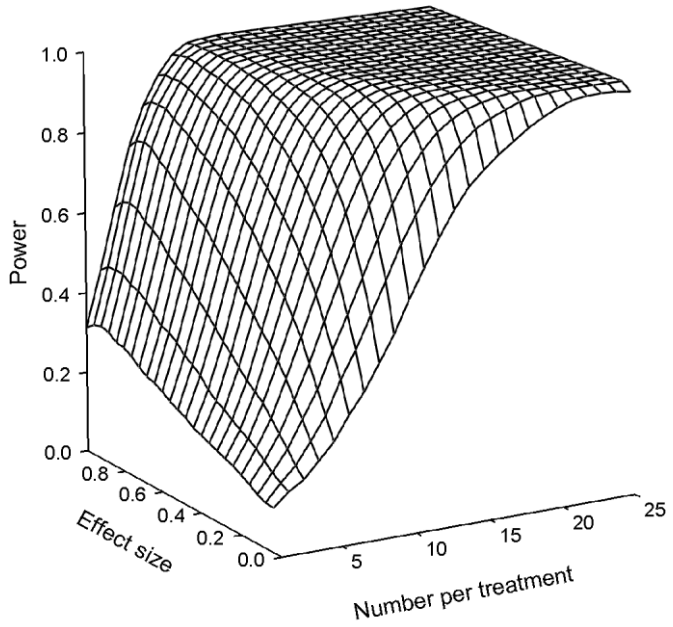

Figure 2.4 Impact of effect size and treatment size on the ability to detect a signal during EIA surveys, the smoothed results of a power analysis. Surveys including up to 10 replicates would detect moderate effect sizes with reasonable power.

This model does not consider spatial autocorrelation within the site as the analysis considered the averaged effect between replicates; we recommend consideration of autocorrelation in future prospective power analysis. Power analysis may not always be helpful: for those studies that may never be able to expand beyond $n = 1$, we propose that analysing the gradient change in distribution across a site and developing forms of randomisation tests and simulations might prove to be more useful (see Seavy and Reynolds, 2007).

2.9 CONCLUSION

An increased reliance on meeting energy requirements with renewable resources will put pressure on the development of alternative technologies, including the exploitation of wave energy. Vital to this will be developing an understanding of the potential ecological impacts that these technologies represent. To date, due to the prevalence of wind turbines, much work has focused on the potential for collision risk (i.e Garthe and Huppop, 2004, Fielding et al., 2006, Fox et al., 2006, Perrow et al., 2006), and the cumulative effect a number of installations may have on migration pathways (Desholm and Kahlert, 2005, Masden et al., 2009, Masden et al., 2010b). For wave-powered MREIs with low operational profiles this risk will be reduced, although with this comes an increased risk of underwater collision.

Wave-powered MREIs are likely to cause some disturbance during construction, maintenance and decommissioning. However, impacts related to construction activities are likely to be minimised in wave-powered MREI which do not require the pile driving associated with current wind technologies. MREIs also have the potential to change environmental processes around the devices indirectly, which in turn may alter habitat assemblages. Disturbance can have deleterious impacts on foraging efficiency, however; if MREIs offer the potential to act as FADs and MPAs then the reverse may be true as birds could profit from an increase in food availability.

With appropriate mitigation, wave-powered MREIs may also enhance habitats through the provision of novel hard substrate and the FAD effects of buoys, which may prove more effective than found with wind-powered MREIs (Wilhelmsson et al., 2006). Unlike wind-powered MREIs, wave-powered MREI structures will provide roosting sites which could help marine birds to exploit an aggregated and protected resource.

The level to which other impacts listed here will affect marine birds is unclear. It is vital to expand this knowledge base which will require the broad-scale acceptance of common methods within the sector in order to develop studies that are comparable. The incorporation of common EIA methods at the early stages of MREI development would allow each site to act as its own control, giving better depth to the assessment of impacts. In developing a better understanding of the potential threats MREIs may pose, ecological principles could be built into MREIs at the development stage, thus allowing for the mitigation of some effects and potentially scaling down the requirement for monitoring programmes in the future. However, a large gap exists in our knowledge of how individual level effects become population level changes (Sutherland, 1996, Elphick, 2008), and without standardised methods the meta-analysis required to investigate potential population level changes are not possible.

We must also consider that renewable energy generation displaces traditional forms of energy production, leading to a positive environmental benefit through a reduction in fossil fuel use. Therefore, any negative impact should be put in the wider context of continued reliance on fossil-fuel powered energy production. MREI impacts are likely to be spatially discrete while the climate impacts from fossil fuels are wide scale and indiscriminate (Stewart et al., 2007, Elphick, 2008, Snyder and Kaiser, 2009).

We re-iterate calls by Gill (2005) and Inger *et al.* (2009) for the integration of multi-disciplinary scientific research to develop an understanding of the implications an expanding MRE industry may have on the environment, and mitigate any threat to the ecology of development areas. Wave-powered MREIs are certain to become a part of the marine environment; however, with appropriate planning, mitigation, and monitoring they have the potential to offer benefits to marine birds in the future.

Chapter 3:
A novel technique to identify important at-sea areas for seabird conservation

This chapter has been accepted for publication by Biological Conservation as part of a special issue on seabirds and marine protected areas:

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Abstract

Seabirds are well monitored and protected at their breeding grounds but spend most of their life at sea, where they are less well monitored and afforded little protection. In an attempt to address this dichotomy, attention has been directed toward establishing a network of marine reserves for seabirds, based largely on information from at-sea surveys and/or biotelemetry studies. Nevertheless, these approaches are costly, are typically only available for a limited number of locations, and not suitable for species that have either poor at-sea detectability or are unable to carry tracking devices. Here we develop a technique to identify important areas for breeding seabirds based on at-sea projections from colonies. Synthesising data from colony surveys with detailed information on population dynamics, foraging ecology and near-colony behaviour, we project colony-specific foraging distributions of the Northern gannet (*Morus bassanus*) at colonies in the UK, Ireland and France. We test the ability of our models to identify at-sea hotspots through comparison with existing data from biotelemetry studies and at-sea visual surveys. These models show a positive spatial correlation with one of the

most intensive at-sea seabird survey datasets. While there are limitations to estimating at-sea distributions of seabirds, implemented appropriately, we propose they could prove useful in identifying potential Marine Protected Areas for seabirds. Moreover, these models could be developed to suit a range of species or whole communities and provide a theoretical framework for the study of factors such as colony size regulation.

3.1 INTRODUCTION

Changes are occurring in the marine environment and, as wide-ranging apex predators acting as bio-indicators of marine systems (Furness and Camphuysen, 1997), seabirds require protection from the deleterious effects of climate change (Grémillet and Boulinier, 2009), fisheries (Pauly et al., 1998, Lewison et al., 2004a, Votier et al., 2004b), pollution (Votier et al., 2005), and offshore development (Inger et al., 2009, Grecian et al., 2010). One of the key tools to alleviate these pressures could be the designation of Marine Protected Areas (MPAs) for seabirds, although this approach has limitations related with the scale of marine systems, the dynamic nature of the oceans, and thus the ephemeral nature of many species. Furthermore, the high costs associated with implementing wide-scale protection will likely force MPAs to be small and targeted for particular species assemblages (Game et al., 2010). This proves problematic for the conservation of species, such as seabirds, that require protection of disparate breeding and foraging grounds (Guilford et al., 2008). Thus, these areas have very different selection criteria for protection and require separate consideration.

Seabird research has historically focused on colony-based studies because, as central-place foragers, seabirds are easily accessed during the breeding season (e.g. Mitchell et al., 2004). Systematic at-sea visual surveys began to address this imbalance in the 1970s (Haney, 1985, Stone et al., 1995), and have provided vital information on the wide-scale distributions of seabirds (e.g. Piatt et al., 2006). However, there are limitations to at-sea surveys, and while they yield large sample sizes, they are usually unable to distinguish colony of origin, age, or the reproductive status of individual birds. Inferring colony level changes from observations in the marine environment is therefore problematic.

The advent of individual-based tracking technology (reviewed by Ropert-Coudert and Wilson, 2005) has shed light on the ecology of seabirds when away from the colony (Wilson et al., 2002, Burger and Shaffer, 2008). Nevertheless, limitations in device size have until recently confined deployments to large species (Phillips et al., 2003), and there may be deleterious effects of both device attachment and handling (Barron et al., 2010). Tracking studies provide detailed ecological information at the individual level, but this is typically available for only a restricted number of locations, and a consensus on the most appropriate method for data analysis is lacking (Wakefield et al., 2009). Consequently, a mismatch exists between colony-based and at-sea studies, a dilemma that greatly inhibits our ability to make decisions on the conservation and management of seabird populations.

In addressing this mismatch, studies have linked both vessel-based visual counts and satellite tracking data to environmental variables in order to aid the delineation of marine IBAs for pelagic foraging seabirds (Amorim et al., 2009, Louzao et al., 2009). In the UK, the JNCC has begun to identify SPAs offshore using the European Seabirds At Sea database (ESAS), which provides long-term, year-round, distributional data on UK seabird populations (Kober et al., 2010). Collaborative marine IBA projects in Spain and Portugal have used these techniques to produce the first complete marine IBA network at a national level, incorporating 59 marine IBAs and gazetting 57,135 km^2 (Ramírez et al., 2008, Arcos et al., 2009, SEO/BirdLife, 2009). These highlight the importance of productive areas, which due to their small to medium-scale repeatability, association with physical features, and established appeal to marine top predators (Hyrenbach et al., 2000, Louzao et al., 2006, Weimerskirch, 2007, Fauchald, 2009, Paiva et al., 2010b) makes them ideal candidates for conservation (Piatt et al., 2006).

An alternative approach for designating protected areas at-sea would be to collate information collected through colony-based counts and project at-sea distributions based on known foraging ranges (BirdLife, 2010b). While this technique lacks the rigour of at-sea surveys or bio-logging studies, it is both inexpensive and quick to implement. Moreover, it can be applied to species for which at-sea detectability is low, or attachment of tracking devices impossible (i.e. for small species). In addition, if foraging projection models were integrated with fundamental ecological principles, it may be possible to create more sophisticated and accurate model predictions that represent realistic estimates of at-sea density distributions.

Here, we develop a model that predicts the at-sea distribution of a central-place forager, the Northern gannet *Morus bassanus* (hereafter gannet) a large and well-studied piscivorous apex predator. Colony-based studies of this species have demonstrated that: 1) foraging range is positively correlated with colony size both across multiple colonies and within a single colony over time (Lewis et al., 2001); 2) population densities are elevated around colonies (McSorley et al., 2003); and 3) foraging behaviour is linked to resource availability (Garthe et al., 2007, Hamer et al., 2007, Votier et al., 2010). We combine this ecological information with data collected on the size and distribution of colonies (Nelson, 2002, Mitchell et al., 2004), building a model that predicts distributions for all UK, Irish, Channel Island and French colonies. We validate these spatial predictions using data from at-sea visual surveys and tracking data. The development of a technique that can accurately predict the spatial distribution of seabirds will be vital in identifying both areas in need of protection, and areas of potential conflict with anthropogenic threats. We consider the utility of this approach for other seabird species and multiple species, enabling a community level approach to seabird conservation.

3.2 MATERIALS AND METHODS

Step 1: Collating information on colony demographics

The gannet is a key species for European conservation as circa 70% of the world population breed around UK, Irish and French shores (Mitchell et al., 2004). Long-term monitoring studies at a number of colonies have provided breeding population estimates, along with detailed ecology of the species. Gannet colony locations and colony sizes were taken from Mitchell et al. (2004) and combined with recent information on Channel Island (Ortac and Les Etacs) and northern French (Rouzic) colonies (Nelson, 2002, Grémillet et al., 2006) (see Table 3.1). We use Apparently Occupied Nests (AONs) as our measure of colony size, which is equivalent to the number of breeding pairs (Mitchell et al., 2004). We build a model in seven steps that first projects a foraging radius around each colony, and then add constraints to the projections through application of current ecological understanding of the species (Figure 3.1).

Step 2: Constraining foraging ranges by population size

Intra-specific competition for resources during the breeding season is believed to be an important factor in regulating colony size for seabirds in general (Furness and Birkhead, 1984), and gannets in particular (Lewis et al., 2001). This within-population competition is typified by the strong positive relationship between colony size and foraging trip duration, and so when projecting foraging ranges we must account for this effect. Information on colony size and location was used to derive a colony specific estimate of foraging distance (*fd*) using the density dependent relationship described by Lewis et al. (2001), where observations at a number of gannetries indicate foraging trip duration, and thus foraging distance (based on Hamer et al., 2000) to be positively

related to colony size (Equation 1). This estimated the foraging distance (*fd*) of colonies based on the square root of colony size in number of pairs (*p*) (Table 3.1).

Equation 1 (Lewis et al. 2001):

$$fd = 0.344\sqrt{p} + 40.062$$

Step 3: Projection of foraging radius from the colony

We combined the colony-specific foraging distances with information on colony location (Table 3.1), to construct a colony-centred foraging radius. This was overlaid upon a high resolution digital elevation model (TerrainBase, National Geophysical Data Centre) to derive the total available area of marine habitat, and exclude any areas of land within range of the colony. The density of breeding gannets was calculated from the colony size (*p*) and area of available marine habitat, to give an estimate of colony-specific foraging effort (pairs km^{-2}). This process was repeated for each colony and summed to give a total population distribution estimate for all colonies (Figure 3.2A). Pairs were assumed to be uniformly distributed across the foraging radius, and so high gannet densities occurred only at the overlap between two or more colonies, or when the foraging range was constrained by local topography.

Step 4: Integration of tracking data

Comparison of our initial foraging distance estimates with mean distances calculated from gannet Global Positioning System (GPS) tracking data suggest the ranges produced using Equation 1 underestimate the total distances travelled. The mean predicted foraging distance across all colonies derived from Lewis et al. (2001) was 69.4 km (range = 40.4 to 124.0 km, Table 3.1, Figure 3.2A.), while gannets tracked

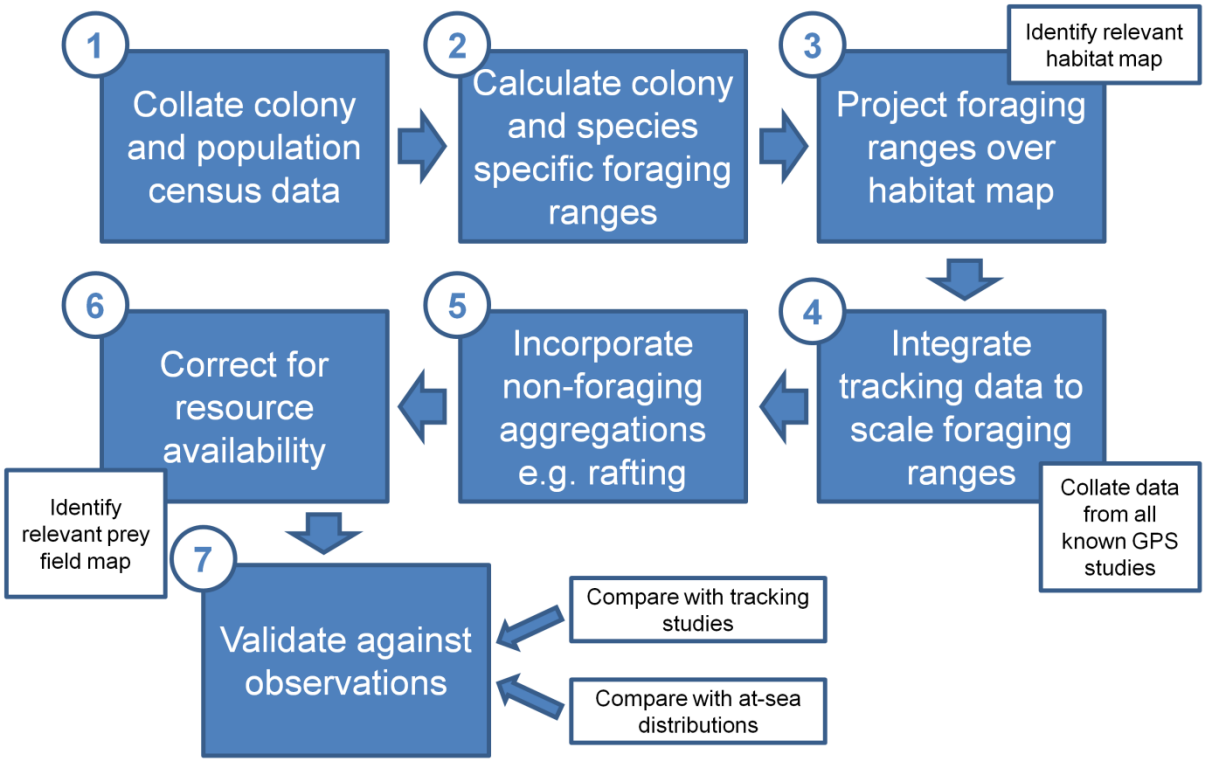

Figure 3.1 Flow chart representing the steps involved in at-sea projection model development. This simple seven-step framework is adaptable to incorporate other data sources, allowing application of this method to different seabird species.

from UK and French colonies between 1998 and 2006 travelled on average up to 150.9 km from the colony (range = 100 to 223 km, Table 3.2). To account for this disparity we use the mean of the ratio of tracked/ predicted calculated from the three colonies for which we have GPS tracking data, multiplying the estimated foraging distance by 1.4. This difference most likely reflects inter-annual differences in resources, and allows the incorporation of environmental conditions *i.e.* the relationship with colony size prevalent in 2000 (Lewis et al., 2001), while also including the accuracy of GPS data to identify foraging locations.

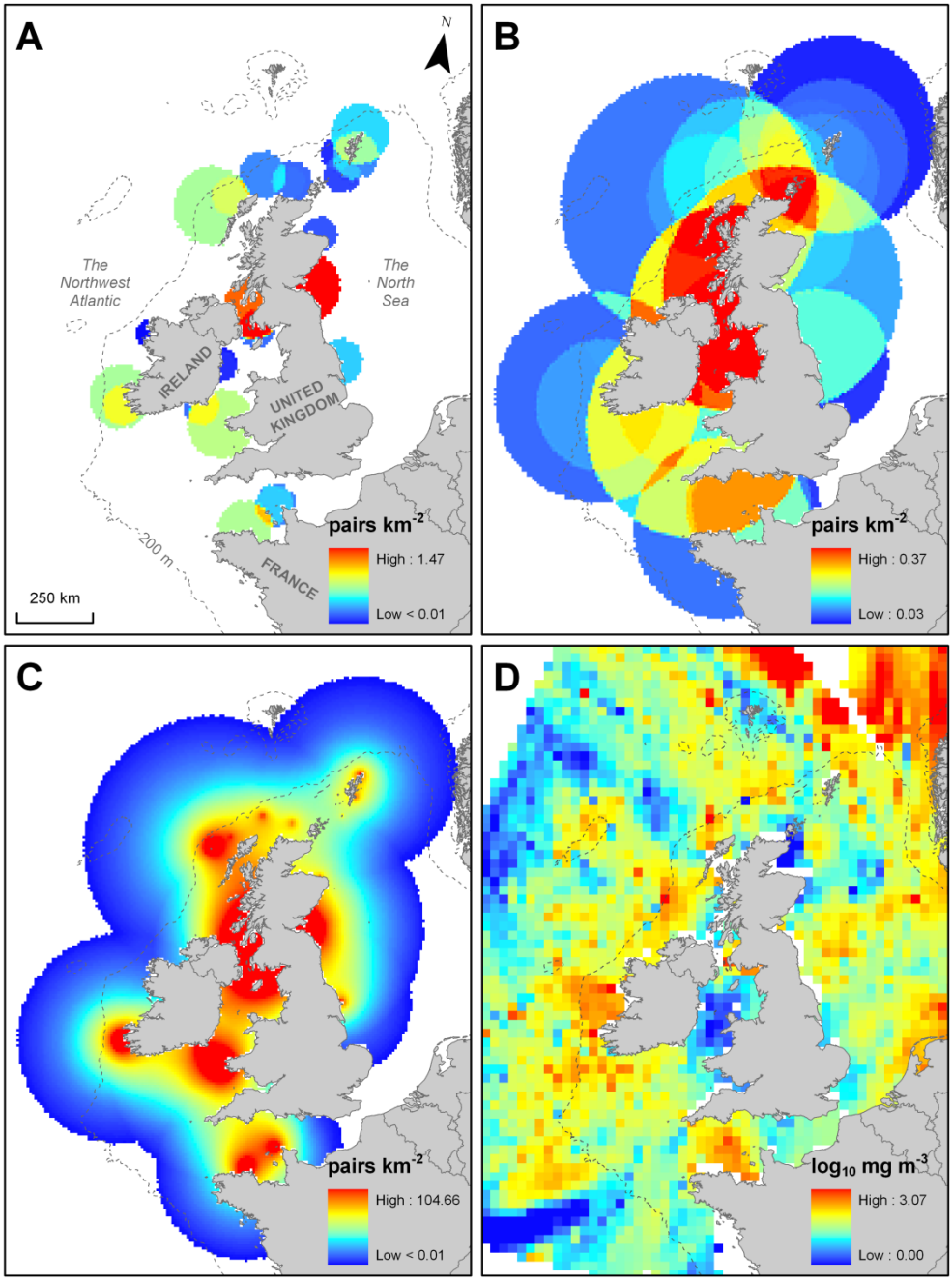

Figure 3.2 Predicted distributions of the northern gannet (*Morus bassanus*) around the UK, Ireland, Channel Islands and northern France. **A)** *Step 1-3:* Information on colony size and location generated foraging radii forming colony-specific foraging areas, density within these areas (pairs km^{-2}) was calculated using the area of ocean circumscribed by the radial foraging arc and the estimated colony size. **B)** *Step 4:* Estimation of maximal foraging ranges derived from tracking studies (see Table 3.2) were used to extend the initial predictions. **C)** *Step 5:* Density was weighted by a log-linear decay function. **D)** *Step 6:* Average June Calanus copepod abundance (log_{10} mg m^{-3}) around the UK and Ireland (1953 - 2002) taken from the SAHFOS continuos plankton recorder.

Colony:	Longitude:	Latitude:	AON (Year):	Foraging range (km):	Maximum foraging range (km):
St Kilda, Outer Hebrides, Scotland	-8.547	57.871	59 622 (2004)	124.0	421.9
Bass Rock, East Lothian, Scotland	-2.631	56.076	48 065 (2004)	115.4	392.7
Grassholm, Pembrokeshire, Wales	-5.486	51.730	39 292 (2009)	108.2	368.1
Little Skellig, Kerry, Ireland	-10.510	51.782	29 683 (2004)	99.3	337.8
Ailsa Craig, Ayrshire, Scotland	-5.122	55.252	27 130 (2004)	96.7	329.0
Hermaness, Shetland, Scotland	-0.926	60.808	24 353 (2008)	93.7	318.8
Rouzic, Brittany, France	-3.436	48.900	17 507 (2005)	85.5	291.1
Sula Sgeir, Outer Hebrides, Scotland	-6.169	59.095	9225 (2004)	73.1	248.7
Noss, Shetland, Scotland	-1.018	60.146	8652 (2003)	72.0	245.1
Bempton, Yorkshire, England	-0.161	54.148	6487 (2008)	67.7	230.5
Les Etacs, Channel Islands	-2.240	49.704	4862 (2005)	64.0	217.9
Sule Stack, Outer Hebrides, Scotland	-4.407	59.085	4618 (2004)	63.4	215.8
Bull Rock, Cork, Ireland	-10.298	51.589	3694 (2004)	60.9	207.4
Roareim (Flannans), Outer Hebrides, Scotland	-7.678	58.284	2760 (2004)	58.1	197.8
Ortac, Alderney, Channel Islands	-2.291	49.723	2547 (2005)	57.4	195.4
Scar Rocks, Wigtownshire, Scotland	-4.705	54.665	2500 (2005)	57.2	194.8
Fair Isle, Shetland, Scotland	-1.629	59.534	2488 (2008)	57.2	194.7
Great Saltee, Wexford, Ireland	-6.613	52.117	2446 (2004)	57.1	194.2
Troup Head, Aberdeenshire, Scotland	-2.310	57.694	1810 (2007)	54.7	186.1
Foula, Shetland, Scotland	-2.112	60.133	919 (2004)	50.5	171.8
Sule Skerry, Outer Hebrides, Scotland	-4.505	59.024	400 (2007)	46.9	159.7
Ireland's Eye, Dublin, Ireland	-6.056	53.408	375 (2007)	46.7	159.0
Lambay, Dublin, Ireland	-6.003	53.497	83 (2007)	43.2	147.0
Clare Island, Mayo, Ireland	-10.048	53.802	3 (2004)	40.7	138.4
St Margaret's Island, Pembrokeshire, Wales	-4.719	51.642	1 (2004)	40.4	137.5

Table 3.1 Details of gannet colonies included in the model; consisting of all UK, Irish, Channel Island and French colonies, the most recent population estimate for that colony (Apparently Occupied Nests), the predicted foraging range derived from Lewis et al. (2001) and the maximum range derived from existing tracking data.

Foraging events tend to occur at the distal part of the track (Hamer et al., 2009), and so we also adjust our foraging ranges by converting mean foraging ranges to maximum foraging ranges to incorporate these behaviours. We corrected our foraging distances to provide estimates of maximum foraging range using the ratio of the mean displacement from the colony, to the maximum displacement from the colony *i.e.* max/mean (Table 3.2). We used the mean of these ratios, 2.4, to convert the transformed foraging distances into maximum foraging distance, giving a final scale parameter of 3.4 (1.4 x 2.4). After adjustment the mean maximum foraging distance across all colonies was 236.1 km (range 137.5 to 421.9 km, Table 3.1, Figure 3.2B.).

Step 5: Incorporation of near-colony maintenance and transiting behaviours

Near-colony areas are important for maintenance behaviours (Wilson et al., 2009), and central-place foragers also spend large proportions of time transiting between the colony and diffuse foraging sites; therefore bird density decreases with increasing distance from the colony, and for gannets this decline takes a log or exponential form (McSorley et al., 2003, Garthe et al., 2011). To incorporate this behaviour, we multiplied the number of pairs within a given cell (calculated in Equation 1) by the inverse scaled log distance from the focal colony (Figure 3.2C). This weighted the waters in close proximity to the colony to be of relatively higher importance due to transiting and maintenance behaviours, thus creating hotspots for gannet densities around a colony (see Figure 3.2C). However it is unlikely in all cases that these are also important foraging locations (Grémillet et al., 2006).

Step 6: Correction of distributions for resource availability

Food availability has been demonstrated to be a good proxy for the at-sea distribution of seabirds (Furness and Tasker, 2000, Kaiser et al., 2006b, Votier et al., 2010), and so in

order to make inferences about the importance of certain areas for foraging, our at-sea projections of seabird abundance were also weighted by resource availability.

Colony:	Predicted range (km):	Year tracked:	Observed range (km):	Ratio observed/ predicted:	Max range (km):	Ratio Max/ Mean:
Bass Rock	115.4	1998[1]	223	1.9	540	2.4
		2002[2]	320	2.8	590	1.8
		2003[3]	155	1.3	276	1.8
Bass year average:			232.7	2.0	468.7	2.0
Grassholm	108.2	2006[4]	120	1.1	404	3.4
Rouzic	85.5	2006[5]	100	1.2	176	1.8
Colony average:			150.89	1.4	349.6	2.4

[1]Hamer et al. 2001; [2]Hamer et al. 2007; [3]Hamer et al. 2009;

[4]Votier et al. 2010; [5]Grémillet et al. 2006

Table 3.2 Summary statistics for tracking data used to inform step 4 of the projection model.

While fine-scale information on the distribution of forage fish is unavailable, other environmental variables can act as a proxy for food availability (Grémillet et al., 2008a, Votier et al., 2010). For gannets, changes in foraging behaviours such as at-sea path tortuosity and derived ground speed are correlated with north-east Atlantic copepod abundance in the month of June (Votier et al., 2010). We constructed a resource field (Figure 3.2D) using long-term data on calanoid copepod abundance (1953 – 2002) (*CA*) taken from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) Continuous Plankton Recorder (CPR) survey (Johns, 2008), the largest multi-decadal near-surface phyto- and zooplankton monitoring programme in the world (Richardson et al. 2006). Although a regime shift occurred in the North Sea during this time altering the composition of copepod species (Beaugrand, 2004), seabird distributions were not overly affected (Grandgeorge et al., 2008). We use a long timescale in order to provide adequate spatial coverage. The resource field was then used to estimate the amount of

time a gannet would spend in a specific cell, using parameters taken from Votier et al. (2010).

Predicted gannet distributions were interpolated (triangle-based linear interpolation) to match the spatial structure of the CPR data (37.0 km^2) (Sims et al., 2006). The speed a gannet would fly through the cell based on copepod abundance was then derived from the relationship described by Votier et al. (2010) (see Equation 2). To calculate the time a gannet spent within each grid cell, the cell size was divided by the speed estimate and scaled to be between 0 and 1. We then multiplied our projected gannet distributions (Figure 2c) by the scaled time estimate, to correct for the availability of resources.

Equation 2 (Votier et al. 2010):

$$Derived\ ground\ speed\ (kph) = -35.710(\log_{10} Copepod\ Abundance) + 39.761$$

For species, such as gannets, reliant on fisheries discards for at least part of their diet (Grémillet et al., 2008b, Votier et al., 2010) data on the location of fisheries taken from the Vessel Monitoring System (VMS) may be important. However at present the spatial and temporal scale of available data means we are unable to model gannet distributions at the scale of this study (Witt and Godley, 2007).

Overall these six steps produced a map of predicted breeding gannet distributions that incorporated: 1) the effect of intra-specific competition, 2) the importance of distant areas for foraging behaviour, 3) near-colony maintenance and transiting behaviours, and 4) the availability of resources within those areas. As we are predicting the distribution of breeding birds, we represent our model as relative abundance of gannet pairs km^{-2}.

Step 7: Validation of predicted at-sea distributions

For comparison with our at-sea projections we used gannet distributional data taken from two sources: data from all known gannet tracking studies in this region, and extraction of interpolated at-sea gannet distributions from the ESAS database managed by the JNCC (Kober et al., 2010).

Gannet tracking data consists of tracks from four colonies: Bass Rock (n = 13 individuals, n = 13 trips), Grassholm (n = 21 individuals, n = 21 trips), Rouzic (n = 20 individuals, n = 20 trips), and Great Saltee (n = 5 individuals, n = 27 trips), three using GPS loggers (Grémillet et al., 2006, Hamer et al., 2009, Votier et al., 2010) and one using satellite telemetry (Hamer et al., 2001). These provide a comprehensive insight into the movements of individual birds at sea, allowing a useful comparison with our predicted distributions (Figure 3.3B). However, the tracking data are used to parameterise the model and so formal validation is not appropriate.

We used ESAS data incorporating observations of gannets made from at-sea ship transects between May and September (1980 - 2005), to best represent the breeding season. These were interpolated using Poisson kriging to account for unequal sampling effort and the inflated number of zero counts (Monestiez et al., 2006), giving an estimate of individual birds per km^2 for the UK fisheries limit (Kober et al., 2010) (Figure 3c). These data include observations of both adults and juveniles. While this does not provide an exact match to population estimates or the spatial extent of our predictions, it does represent the most accurate available record of the spatial distribution of gannets in UK waters. We quantitatively compared the ESAS database and our predictive models of density with a Spearman's rank correlation, using only cells where an observed and predicted value were available, including zero counts.

ESAS data were interpolated to match 37 km^2 spatial resolution of model outputs. Seabird distributions are likely to be spatially auto-correlated and so we bootstrapped the test by sampling a random 10% of the dataset for the correlation, and iterated this process 10,000 times. Results are therefore presented as mean *p* and r_s (± std.). All analyses were carried out in MATLAB (R2009b, Mathworks) and ArcGIS 9.3 (ESRI, USA).

3.3 RESULTS

The final output of our model estimates the at-sea distribution of all gannets breeding at colonies in the UK, Ireland, Channel Island and France (Figure 3.3A). Distributions are weighted by near colony attendance and resources, so that high densities occur around gannetries and at areas of high copepod abundance.

3.1 Comparison of predicted distributions with tracking data

Gannets tracked in 2006 from Grassholm foraged exclusively to the south and west of the colony but did not venture north of the Celtic Sea Front into the Irish Sea. Gannets tracked from the southern Irish colony of Great Saltee also foraged predominantly to the west of the colony and within 100 km of the southern Irish coast, but did not overlap with birds tracked from Grassholm (Figure 3.3B). Our projected distributions show a similar pattern; the paucity of copepods lowering gannet densities in the Irish Sea, and the productive zone around the Celtic Sea Front elevating densities (Figure 3.3A).

Grémillet et al. (2006) demonstrated a preference in gannets for productive/ mixing zones by linking GPS tracks with the tidal front between eastern and western Channel waters. Our predicted distributions for the Channel centre around the Rouzic colony, but are skewed east by the presence of the Channel Island colonies of Ortac and Les Etacs

which together represent 7409 breeding pairs (Table 3.1). Hamer et al. (2009) found strong associations between foraging behaviour and the tidal mixing front to the east of Bass Rock. The copepod data show a latitudinal gradient in a similar area to this front (Figure 3.2D), that lower gannet densities in the region north east of the colony compared with predictions from earlier models (see Figure 3.2).

Comparison of predicted distributions with ESAS data

Our predictions of habitat use by breeding northern gannets developed using an integrated modelling approach show a statistically significant correlation with the ESAS dataset (Spearman rank correlation, $r_s = 0.459 \pm 0.130$, $p < 0.001 \pm 0.002$, Figure 3.3A and C). To investigate the relevance of the different development steps in the model we also compared outputs from the other model steps with the ESAS data. There were weak correlations between the ESAS data and both Step 3 ($r_s = 0.137 \pm 0.051$, $p = 0.033 \pm 0.067$, Figure 3.2A) and Step 4 ($r_s = 0.126 \pm 0.051$, $p = 0.003 \pm 0.015$, Figure 3.2B). The output from Step 5, the model not corrected for copepod availability (Figure 3.2C), also showed a statistically significant correlation with the ESAS dataset (Spearman rank order correlation, $r_s = 0.326 \pm 0.084$, $p < 0.001 \pm < 0.001$), but did not produce a better fit than the final model.

To test the importance of adjusting foraging ranges in Step 4 we carried out a sensitivity analysis. The foraging ranges input into the model were varied by ± 25% and the final model outputs tested against the ESAS data (Figure 3.4). Varying the foraging range of each colony had very little influence on the final output, which still showed a statistically significant correlation with the ESAS dataset ($r_s = 0.455 – 0.486$, $p < 0.001$, Figure 3.4).

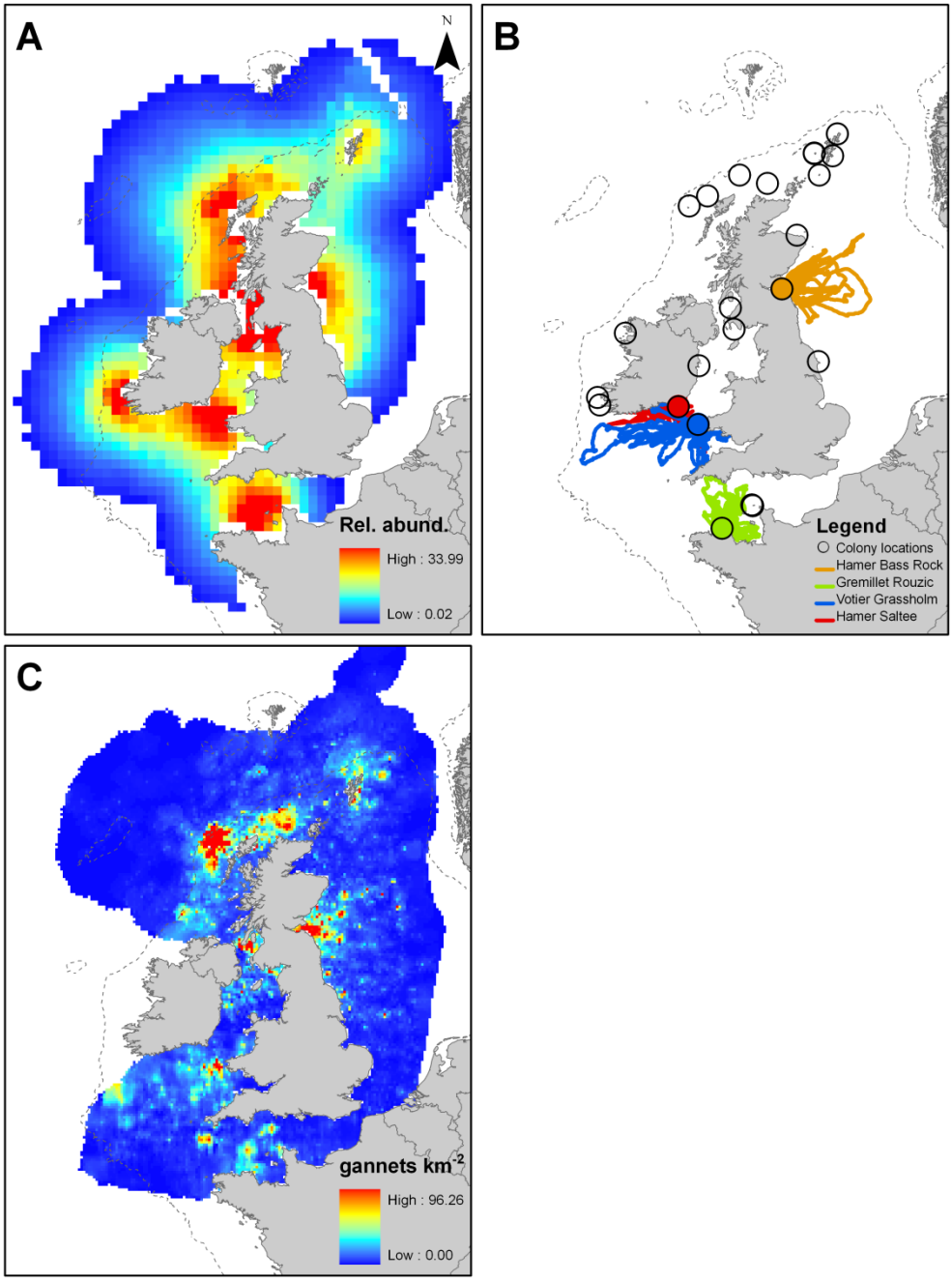

Figure 3.3 Comparison of predicted distributions with collated tracking and ESAS distributional data. **A)** Relative abundance of breeding gannets as predicted by the at-sea projection model. **B)** Location of gannetries around the UK, Ireland and northern France overlayed with tracking data taken from four colonies (Grémillet et al. 2006; Hamer et al. 2009, 2001; and Votier et al. 2010). **C)** The at-sea breeding season distribution of gannets using data taken from the JNCC European Seabirds at Sea database for the last 25 years, interpolated to give density of individuals per km^2 (Kober et al. 2010).

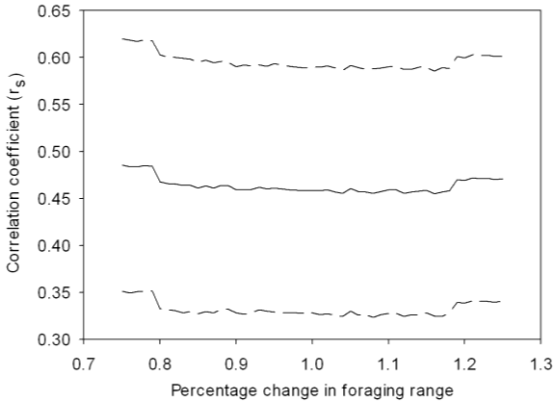

Figure 3.4 Sensitivity of the correlation between the ESAS dataset and model outputs to changes in the foraging range estimate input into the model at Step 4. Adjusting the foraging range estimate for each colony by ± 25% had very little effect on the similarity of the model output to the ESAS dataset.

During ESAS surveys more gannets are seen due to transiting and maintenance behaviours around colonies, and gannet distributions around colonies are elevated using the log-linear decay function. The data also highlight some important offshore areas; the Hebridean shelf break appears to aggregate gannets in both the ESAS data and our predictions, but this could be due to the occurrence of a number of colonies in the area. Broadly, both techniques suggest similar areas of low gannet density in areas such as the Rockall plateau, Orkney, north-east North Sea, the eastern English Channel, the Celtic Sea and the South West approaches. These areas have few or no gannetries, and visual comparison with data on copepod abundance (Figure 3.2D), suggests they may be poor foraging areas. Nevertheless, the Celtic Sea and South West approaches support large fisheries for pelagic and demersal fish (Witt and Godley, 2007) which may provide a food resource to gannets and other seabirds (Votier et al., 2004b).

3.4 DISCUSSION

We present a method that, based on our current understanding of gannet foraging behaviour, quickly and effectively highlights important at-sea regions. Data collected from at-sea visual surveys has been vital in estimating habitat use on broad temporal and spatial scales, and while tracking data provides fine scale spatial information, sample sizes are comparatively small and it is improbable that data will ever be collected from all seabird colonies. In contrast, our approach predicted distributions for 25 gannetries, totalling 299,522 pairs of breeding birds and representing circa 70% of the global breeding population (Mitchell et al., 2004). Moreover, adaptation of these models for other central-place foragers, as well as multiple species, could provide an integrated framework to guide both the siting of future MPAs for seabirds, and the mitigation of offshore construction activities, fisheries management and oil pollution events through marine spatial planning.

There are few other syntheses of tracking and colony-based studies, but our results suggest that the models are robust and comparable to the observed distributions of gannets at sea. Differences in distribution between the ESAS data and our predictions may be due to our exclusion of the German, Norwegian and Faroese colonies. Birds from these are all capable of foraging within UK and Irish waters, although the colonies are much smaller. Our models also exclude immature birds, which the ESAS data include, this age class may comprise >50% of the population and are highly vagile (Votier et al., 2011). Nevertheless, the efficiency of this technique also allows modelling of species traditionally hard to study at sea, and offers obvious benefits as a technique when compared to at-sea studies and tracking studies (Louzao et al., 2009). By emphasising the importance of near colony areas with a log-linear decay, and including distributional changes due to resource availability, our models highlight

important areas at the colony level both in the near-shore and offshore. Nevertheless, the distributions predicted by models with and without resource characterisation are very similar suggesting that other proxies may be more appropriate, or that calanoid copepod and fish abundances are not correlated spatially. The importance of this step will be highly species specific. This technique integrates all at-sea activities, and so any MPA that would arise from this approach would protect transiting and foraging activities. Areas of importance specific to foraging could be identified through, for example, Area Restricted Search analysis of individual GPS data (Fauchald and Tveraa, 2003).

There are limitations to projecting at-sea distributions of seabirds in this way. The decay and resource weighting techniques may not capture seabird movements adequately, but do provide a framework for the future development of this technique. Furthermore, gannets are known to alter foraging behaviour relative to prey abundance and distribution (Garthe et al., 2007, Montevecchi, 2007, Montevecchi et al., 2009), and so foraging distance and trip duration are not always correlated (Garthe et al., 2011). Resources also move throughout the breeding season, potentially altering small-scale distributional patterns. Information from tracking studies could be used to inform near-colony distributions *i.e.* through kernel analysis or a lattice-based approach (Barry and McIntyre, 2011), but these are highly species and colony specific (McSorley et al., 2003, McSorley et al., 2008, Wilson et al., 2009), and not available for species unable to carry devices. Furthermore, there is no direct trophic link between gannets and copepods, and as copepod and fish abundances may be poorly correlated spatially it may be inappropriate to use a planktonic resource map to infer the distribution of a piscivorous plunge-diving seabird (Grémillet et al., 2008a). While gannets are known to feed on a range of prey including mackerel, garfish, herring, sandeel and fisheries

discards (Nelson, 2002, Votier et al., 2010, Garthe et al., 2011) at present spatially resolved fish abundance data are not widely available at this scale, but there is scope to combine log book and VMS data to provide such information (Bertrand et al., 2008).

In the absence of *in situ* estimates of prey availability remote-sensing data can be employed as a proxy to define important foraging habitats for seabirds, but should be used cautiously (Grémillet et al., 2008a). The flexibility of our model permits the incorporation of more appropriate resource maps in the future. Previous identification of pelagic IBAs for seabirds collated a range of information on not only seabird distributions but also habitat availability. These included; bathymetry, distance to features such as the coast, shelf-break and colonies, remotely sensed chlorophyll-a, and sea surface temperature (SST), and identification of both large-scale and local fronts (SEO/BirdLife, 2009). Nevertheless, our model was not sensitive to changes in foraging range estimates; the results of a sensitivity analysis (Figure 3.4) varying foraging ranges by ± 25% produced a model statistically comparable with the ESAS data set.

When implementing protection for wide ranging and pelagic seabirds, it will be important to protect features of known importance to the targeted species. Thermal fronts, upwellings, mixing zones, and other tidal features (Tew Kai et al., 2009) are known to provide food resources and exhibit a high degree of spatial and temporal predictability (Game et al., 2009). Recent developments in composite front maps could allow the tracking of marine animals through dynamic systems in virtual real-time (Miller, 2009), allowing detailed analysis of an animal's response to these systems. Indeed, relating biology to consistent marine features would allow MPA design to be linked to bathymetry, aiding implementation and enforcement (Hyrenbach et al., 2006).

Seabird conservation requires a multi-faceted approach, involving not only protection at the nest site, but also consideration of near-colony rafting aggregations, safeguarding of foraging stock through protection of pelagic foraging zones, and consideration of the wintering grounds. Indeed the protection of over-wintering areas is important for both winter foraging and staging (Guilford et al., 2009), and population mixing (González-Solís et al., 2007). The wintering grounds of gannets breeding in the UK and France, and many other key populations of European seabirds are mainly outside the EU. Therefore, while similar tools (biotelemetry, at-sea surveys and modelling) can be utilised to define the winter habitats of these species, protecting these areas will require international cooperation. For wide-ranging species, international cooperation has aided the protection of breeding season foraging grounds (*e.g.* the Agreement on the Conservation of Albatrosses and Petrels), and tracking could prove vital in quantifying the utilisation of marine sanctuaries by target species, and enforcing vessel compliance (Hyrenbach et al., 2006, Pichegru et al., 2010a).

The development of precise distributional models provides a framework for testing population level processes. Perturbations such as environmental change, pollution events, or offshore construction could be simulated to investigate demographic responses at specific colonies. The projection of accurate colony-specific distributions could also allow investigation of the potentially regulatory effect that the near-colony marine environment has on colony-level processes (Ashmole, 1963), or the density dependence due to the proximity of other colonies (Furness and Birkhead, 1984), and could be applied to a number of other centrally-placed marine predators.

A network of protected areas is required to mitigate the threats facing seabirds, and this approach not only offers a timely method to draw attention to potentially important

ocean habitats for seabird conservation, but also provides a theoretical framework to advance our understanding of the intrinsic and extrinsic factors that influence colony demographics.

Chapter 4:
Consistent wintering behaviour and carry-over effects in a marine predator

Abstract

Individual fidelity to particular wintering locations is potentially widespread among migratory animals, yet is relatively poorly understood. Locating the optimum habitat during the non-breeding period is crucial for an individual to replenish resources lost during the previous breeding attempt, and therefore should be under strong selection. Indeed there is increasing evidence to suggest that the consequences of wintering habitat selection may carry-over to impact individuals in subsequent seasons. For marine vertebrates, while resources show high spatio-temporal variability at small scales, they occur within regions that are consistently productive at large-scales. Individual consistency in migratory strategy may allow individuals to return repeatedly to known foraging grounds. Furthermore, the development of persistent individual foraging specialisations may reduce competition during the wintering period. We combine two approaches to study the wintering behaviour of a migratory marine predator, the Northern gannet *Morus bassanus*: the use of geolocation sensors (GLS) to track individuals over multiple seasons, and the analysis of stable isotope ratios in consumer tissues to provide information on dietary preferences during the wintering period. This approach allows us to spatially resolve dietary information, and so compare foraging strategies both between and within wintering locations. We describe the migration strategies of gannets from two breeding colonies in the north-west Atlantic, and demonstrate that (1) individuals are consistent in both the location and size of wintering ranges across consecutive seasons, (2) the isotopic values of feathers grown in

consecutive winters are highly repeatable, (3) there are within-wintering location and between-individual isotopic differences that (4) reflect individually consistent strategies. Moreover (5), these strategies affect both the timing of arrival at the breeding colonies and body condition, which may have fitness consequences. We conclude that gannets adopt individual migratory and foraging specialisations that persist over multiple years, potentially allowing individuals to target heterogeneously distributed resources repeatedly during winter. These strategies interact with seasonal conditions and so have consequences for individual condition and phenology in the subsequent breeding season. These patterns may arise to reduce competition for resources such as food and space during the non-breeding period, or be the result of heritable migratory traits.

4.1 INTRODUCTION

Migration is a widespread phenomenon and the ability of individuals to move between habitats, and so rebuild their body condition, is a key element of many life-history strategies. Many animal groups migrate thousands of kilometres between discrete breeding and non-breeding grounds, and exhibit strong fidelity to particular wintering locations. Nevertheless, while breeding site philopatry has been the focus of much study, an inability to record individuals over multiple seasons and at the global scales associated with migration has hindered our understanding of the potential causes and consequences of philopatry (Koenig et al., 1996). The study of wintering distributions has in the past relied on the recovery or re-sighting of marked individuals (Hestbeck et al., 1991, Berthold, 2001, Wernham et al., 2002, Godley et al., 2003), which may be biased by spatio-temporal variation in band recovery (Mehl et al., 2004) or band effects (Saraux et al., 2011). The recent advent of individual based tracking technology, and the proliferation of miniaturised logging devices (Ropert-Coudert and Wilson, 2005, Tomkiewicz et al., 2010) has instead enabled researchers to track individuals of known provenance, status and sex over extended periods and geographic scales (Phillips et al., 2005b, Alerstam et al., 2006, Broderick et al., 2007, Egevang et al., 2010).

Wintering fidelity may allow individuals to become familiar with the spatial availability of resources such as food and shelter, or predator distributions (Hestbeck et al., 1991). Indeed, studies of breeding habitat selection indicate that when resources are distributed heterogeneously across habitats the cost of changing strategies and moving to an unknown area is high (Switzer, 1993, Doligez et al., 2003), and the same mechanisms may apply to winter habitat selection. Evidence for winter philopatry has been documented in a range of taxa, including passerines (Cuadrado et al., 1995), anatidae (Hestbeck et al., 1991), cetaceans (Calambokidis et al., 2001), pinnipeds (Bradshaw et

al., 2004), seabirds (Phillips et al., 2005b, Phillips et al., 2006), sea turtles (Broderick et al., 2007, Schofield et al., 2010, Hawkes et al., 2011) and sharks (Jorgensen et al., 2010). Nevertheless, few studies documenting the potential consequences of philopatry exist. Understanding these strategies is a key question in ecology, because the conditions experienced by an individual during the non-breeding period will directly impact the capacity to replenish body reserves after a breeding event, and have consequences for both survival probability and the ability to reproduce in the following season (Crossin et al., 2010, Harrison et al., 2010). Ecologists have long been aware that individuals might show carry-over effects from one season to the next (Fretwell, 1972, Sutherland, 1996), but the difficulties involved in following individuals over large distances and annual cycles have, until recently, made these theories hard to test (Marra et al., 1998). A recent review suggests carry-over effects may be much more widespread than previously thought (Harrison et al., 2010).

For marine vertebrates, wintering fidelity may allow individuals to mitigate the patchy nature of prey by returning to broadly productive regions such as thermal fronts, upwellings, mixing zones and other tidal features (Tew Kai et al., 2009) that are known to provide food resources and exhibit a high degree of spatial and temporal predictability (Phillips et al., 2005b, Weimerskirch, 2007, Fauchald, 2009). The limited data available for migrant seabirds indicate that they usually return repeatedly to the same wintering region, particularly if it is highly productive, but use different intermediate staging (stop-over) sites or vary in timing of movements, presumably responding to changes in local prey abundance (Phillips et al., 2005b, Phillips et al., 2006). Not all species behave in this way however. In a recent study of Cory's shearwaters *Calonectris diomedea*, 36% of tracked individuals changed their main wintering area in successive years (Dias et al., 2011).

Inter- and intra-specific competition for resources during the non-breeding period may be mitigated by spatio-temporal isolation (Croxall et al., 2005, Phillips et al., 2005b) or individual specialisation and behavioural diversification, allowing the exploitation of different niches through consistent inter-population differentiation (Bolnick et al., 2003, Hjernquist et al., 2009, Bergmüller and Taborsky, 2010). Individuals may also operate within the same foraging niche across seasons (Cherel et al., 2007), or may exhibit sex and age dependent niche shifts (Bailleul et al., 2010). Therefore, consistent individual differences in both habitat preference and foraging behaviour during the non-breeding period could mediate intra-specific resource partitioning (Hyrenbach et al., 2002, Phillips et al., 2005a, Phillips et al., 2005b), so reducing competition for limited resources such as food or space (Bolnick et al., 2003, Bergmüller and Taborsky, 2010).

Stable isotope analysis provides a useful tool to examine migration strategies, habitat preference, and diet choice during the non-breeding period (Cherel et al., 2006, Phillips et al., 2009). Studies using stable isotopes have documented the long-term persistence of individual foraging specialisations in a range of air-breathing marine vertebrates including sea otters (Newsome et al., 2009), seabirds (Bearhop et al., 2000, Bearhop et al., 2006, Cherel et al., 2007, Woo et al., 2008) and pinnipeds (Cherel et al., 2007). Sampling over consecutive seasons has demonstrated high individual repeatability in the tissue isotope values of both terrestrial (e.g. Hjernquist et al., 2009) and marine species (e.g. Bearhop et al., 2000, Phillips et al., 2007, Woo et al., 2008).

Although stable isotope data can help answer many ecological questions, using this approach to identify patterns at small spatial scales, and to discriminate between foraging locations and prey types is problematic. Therefore, without information on the location of an individual it is impossible to determine if observed isotope values are

repeatable because individuals winter in the same area and forage on the same prey in successive years, or individuals winter in different locations and forage on different prey in successive years but, in combination, this results in the same isotopic signature. Equally, while data-loggers can provide detailed information on movement and at-sea activity patterns, they provide no information on diet.

The combination of bio-logging and stable isotope analysis provides detailed information on individual migration strategies and foraging specialisations over multiple seasons (Furness et al., 2006) and presents a method to discriminate between the effects of foraging location and prey type on the isotopic signature of an individual (Hjernquist et al., 2009). Furthermore, linking this with data collected during the breeding season allows the potential consequences of individual migration strategies to be elucidated. Despite the obvious advantages of such an approach, there are few published studies either combining these techniques (but see Furness et al., 2006, Phillips et al., 2007, Bailleul et al., 2010) or investigating the potential consequences of winter site fidelity (but see Zbinden et al., 2011).

Here we use data-loggers to provide information on movement and habitat utilisation during the non-breeding period, and stable carbon and nitrogen isotopes to provide information on diet. The combination of these two techniques allows us to spatially resolve dietary information, and so compare foraging strategies both between and within wintering regions. We describe the migration strategies of an apex marine predator, the northern gannet (*Morus bassanus*), from two breeding colonies in the north-west Atlantic, and address a number of key questions: (1) how consistent is individual winter habitat use between seasons, (2) how repeatable are isotope values of tissues across seasons and annual cycles, (3) to what degree do individuals from specific

wintering sites differ isotopically, and (4) do differences in migration strategy or wintering location carry-over to impact two fitness proxies: timing of arrival at the breeding colonies, and body condition?

4.2 METHODS

Deployment of geolocators

In June 2008, we deployed 40 mk7 British Antarctic Survey (BAS) geolocation sensors (GLS) on adult gannets breeding at Rouzic, France (48.900°N, 3.436°W) a colony of circa 17,500 breeding pairs (Grémillet et al., 2006). In July 2009 we deployed 20 mk5 BAS GLS on adults breeding at Grassholm, Wales (51.730°N, 5.486°W) a colony with circa 39,000 breeding pairs (Murray, 2009). Birds were selected at random, away from the edge of the colony and caught under licence using either a brass noose or crook, attached to the end of a pole. Data-loggers were attached to a plastic ring using two cable ties and fitted to the tarsus. The total device mass did not exceed 10 g, representing < 0.4% of adult body mass. During 2010, 21 loggers (52.5%) were retrieved from Rouzic and 13 (65%) from Grassholm, providing data on two complete winter periods for 21 birds, and one complete winter period for 13 birds.

Analysis of location data

Positional information was calculated from logger data following standard methods (Wilson et al., 1992, Phillips et al., 2004). Briefly, geolocation relies on estimating the timings of sunset and sunrise using set thresholds in the light curves recorded by the data-logger. Latitude can be derived from day length, and longitude from the timing of local midday, and midnight, with respect to Greenwich Mean Time and Julian day, providing two positions per day with an accuracy of circa 186 ± 114 km (Phillips et al.,

2004). However, around the vernal and autumnal equinoxes day and night are of equal length, and so it becomes impossible to estimate latitude.

Light curves were analysed using BAS TransEdit and BirdTracker software. On the basis of calibration data from fixed points, and knowledge of likely wintering areas relative to land masses, a light threshold of 10 and an elevation angle of -4.0° were used for processing files, with the exception of those from two loggers in which the epoxy had clouded by the time of retrieval, for which an elevation angle of -3.5° was deemed to be more appropriate. We removed obviously erroneous locations associated with interference in light curves around the time of sunset and sunrise. Location errors can occur through shading of the tag and during equinox periods. All positions recorded up to 10 days either side of the equinox were removed, as well as any fix obviously affected within four weeks of the equinox. Filtering removed 33.7 ± 7.9% of fixes. Validated data were smoothed twice to reduce the error associated with geolocation (Phillips et al., 2004).

A 500 km boundary from the colony was used to separate the breeding and wintering periods as this represents the maximum foraging extent of birds during chick rearing (Guilford et al., 2009, Votier et al., 2010). Departure and arrival were designated as the occurrence of two or more positions outside or inside the 500 km boundary, those individuals never consistently more than 500 km from the colony were assigned as resident. In order to map distributions of resident individuals and those that crossed the boundary during the equinox, the winter period was defined as the average departure and arrival days for the migratory population. These individuals were excluded from any analyses involving chronology.

Wintering locations were identified from kernel analysis in an European Albers equal-area conic projection, the smoothing factor (h) calculated by least-squares cross validation of all wintering locations was 71.3 km. We extracted the wintering period centroid (the central point of all locations) to allow a comparison of individual level site fidelity between years (Broderick et al., 2007, Hawkes et al., 2011), and calculated individual migration distances as the distance by sea between the colony and the centroid winter location. The centroid wintering location represents a geographically corrected average, and so if individuals were to spend an equal amount of time on either side of a landmass the centroid would be between the two.

Stable isotope analysis

Gannets perform a complete annual moult after the breeding season (Ginn and Melville, 1983) and as feathers are metabolically inert after formation, the isotopic ratios of primary and body feathers were assumed to primarily represent prey consumed at the wintering grounds. Feathers were sampled from all Rouzic birds as devices were retrieved, and birds tracked from Grassholm were sampled both pre- and post-deployment. This provided data over one annual cycle for Rouzic, and two annual cycles for Grassholm. To remove any contaminants, feathers were first washed in weak detergent solution then rinsed in 2:1 Chloroform:Methanol (Paritte and Kelly, 2009). Once dry, 5 mm was cut from the tip of each primary (excluding the rachis) and homogenised; for body feathers 5 mm was sampled from the tip of 3 or 4 body feathers and homogenised, and then ~0.7 mg weighed into a tin cup.

Analysis of samples was conducted at the East Kilbride Node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility via continuous flow isotope ratio mass spectrometry, using a Costech (Milan, Italy) ECS

4010 elemental analyser interfaced with a Thermo Electron (Bremen, Germany) Delta XP mass spectrometer. Stable isotope ratios are reported in δ notation, expressed as parts per thousand (‰) deviation according to the equation $\delta X = [(R_{sample}/R_{standard})-1] \times 1000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and $R_{standard}$ is the ratio of the international references PDB for carbon and AIR for nitrogen. The measurement precision, calculated as the standard deviation associated with multiple analyses of internal standards, was ± 0.09‰ for $\delta^{13}C$ and ± 0.11‰ for $\delta^{15}N$. The isotopic composition of animal tissues reflect those of prey consumed during tissue formation, and ratios of $^{15}N/^{14}N$ ($\delta^{15}N$) show a step-wise enrichment (circa 3-5‰) with each trophic level, individuals with higher values of $\delta^{15}N$ therefore generally feed on higher trophic level prey. Ratios of $^{13}C/^{12}C$ ($\delta^{13}C$) also show a small trophic enrichment (circa 0.5-1‰), but are more widely used as spatial markers, including information on the relative reliance of inshore and offshore waters, and between benthic and pelagic regions (Hobson et al., 1994, Cherel and Hobson, 2007, Inger and Bearhop, 2008). Here, we use isotopic signatures to determine how individuals are distributed along these gradients, and the degree to which they are repeatable across years.

Body condition indices

Adopting different wintering strategies may have consequences for body condition, and we therefore calculated the Body Mass Index (BMI) of all captured birds. We measured flattened wing chord, as one of the most reliable measures of skeletal size, and recorded body mass to the nearest 50 g. Two birds had mass measures outside the natural range based on their wing length, possibly due to observer error or because they had not yet fed their chick, and so were excluded from the analysis. BMI was measured as the residuals from a regression of body mass against wing length ($F_{1, 30} = 16.1$, $p < 0.001$, $R^2 = 0.35$), expressed as a percentage of predicted mass, providing a measure of mass

corrected for size (Bolton et al., 1991). We use BMI and the date of arrival at the breeding colonies as our two measures of fitness (Bêty et al., 2004, Schulte-Hostedde et al., 2005).

Statistical analysis

To determine the degree of individual winter site fidelity, we extracted the longitude and latitude of the winter centroid, and calculated the size of the 25% kernel of the winter distribution occupied by birds tracked in both 2008/09 and 2009/10. The repeatability in these traits was calculated using linear mixed models, providing a measure of across-year repeatability (r) with associated standard errors and *p* value (Nakagawa and Schielzeth, 2010).

To determine the degree of individual dietary consistency in wintering areas we calculated the repeatability of $\delta^{15}N$ and $\delta^{13}C$ sampled from both primary and body feathers. To correct for potential temporal differences in baseline isotopic values, we mean-centred isotope values before calculating linear mixed model repeatability estimates (Nakagawa and Schielzeth, 2010). To determine if the isotopic ratios of feathers differed between wintering locations we grouped birds by region and compared $\delta^{15}N$ and $\delta^{13}C$ ratios between core wintering areas using MANOVA.

We used Generalised Linear Mixed Models (GLMMs) fitted using maximum likelihood to investigate the potential carry-over effects of migration distance and tropic position ($\delta^{15}N$) on the timing of arrival. Individuals from Rouzic, but not Grassholm, were tracked for two successive years providing two arrival times, and so we fitted individual and year as separate random factors and included colony interactions. BMI measurements were only available for the 2010 season and so we did not consider year

effects. The potential carry-over effects of migration distance, and $\delta^{15}N$ on BMI were instead modelled using Generalised Linear Models. For all models, we first fitted the fully parameterised model, and then removed terms by sequential deletion while testing for significant changes to model variance (Crawley, 2007). To assess the biological relevance of GLM results we present R^2 values, for GLMMs fitted using maximum likelihood we calculate Nagelkerke pseudo-R^2 (Nagelkerke, 1991). All analyses were carried out in ArcGIS 9.3 (ESRI, USA), MATLAB R2009b (The Mathworks, USA), and R 2.11.1 (R Development Core Team, Austria).

4.3 RESULTS

Winter distribution

During the winter period, gannets utilised a broad range of oceanographic regions, from the North Sea to the coast of Mauritania, and from the Canary Islands to the west coast of Syria (Figure 4.1). We categorised wintering areas by comparing the wintering destination during 2009/10 in relation to the Straits of Gibraltar (36°N meridian), individuals were then split into Northern (Resident), Southern (West African), and Mediterranean migrants. The proportion of individuals from the two colonies using each area was not statistically different ($\chi^2_2 = 4.459$, $p = 0.108$, Table 4.1), but over twice as many birds tracked from Grassholm wintered off the coast of West Africa (69.2%) compared to those tracked from Rouzic (33.3%). Individuals tracked from Rouzic were more equally distributed among the wintering areas and occupied a larger overall range (75% kernel area = 2,586,772 km^2) than individuals from Grassholm (75% kernel area = 1,127,619 km^2). Furthermore, the distribution of Rouzic individuals across wintering locations did not differ between years.

Winter Area	Rouzic 2008/09	Rouzic 2009/10	Grassholm 2009/10
North (Resident)	38.1%	38.1%	23.1%
Mediterranean	28.6%	28.6%	7.7%
South (West Africa)	33.3%	33.3%	69.2%
Total individuals:	21	21	13

Table 4.1 Distribution of gannets between wintering regions, defined by comparing the location of the core over-wintering area (25% kernel) in relation to the Straits of Gibraltar (36°N meridian).

Consistent winter location and range size

Individuals from Rouzic were tracked throughout two successive winters, during which they displayed very strong site fidelity (Figure 4.2). Both the centroid latitude ($r = 0.964 \pm 0.024$, $n = 21$, $p < 0.001$, Figure 4.3A) and centroid longitude ($r = 0.972 \pm 0.019$, $n = 21$, $p < 0.001$, Figure 4.3B) were highly repeatable between years. The mean straight-line distance between consecutive winter centroids was 308.6 ± 316.7 km (range = 23 – 1082 km, Figure 4.2). Furthermore, the size of core winter ranges differed considerably among individuals (25% kernel range = 14,821 – 70,229 km^2), and were highly repeatable between years ($r = 0.609 \pm 0.150$, $n = 21$, $p < 0.001$, Figure 4.3C). This indicates that individuals not only exhibit high levels of fidelity to wintering areas, but also occupy similarly-sized ranges in consecutive years.

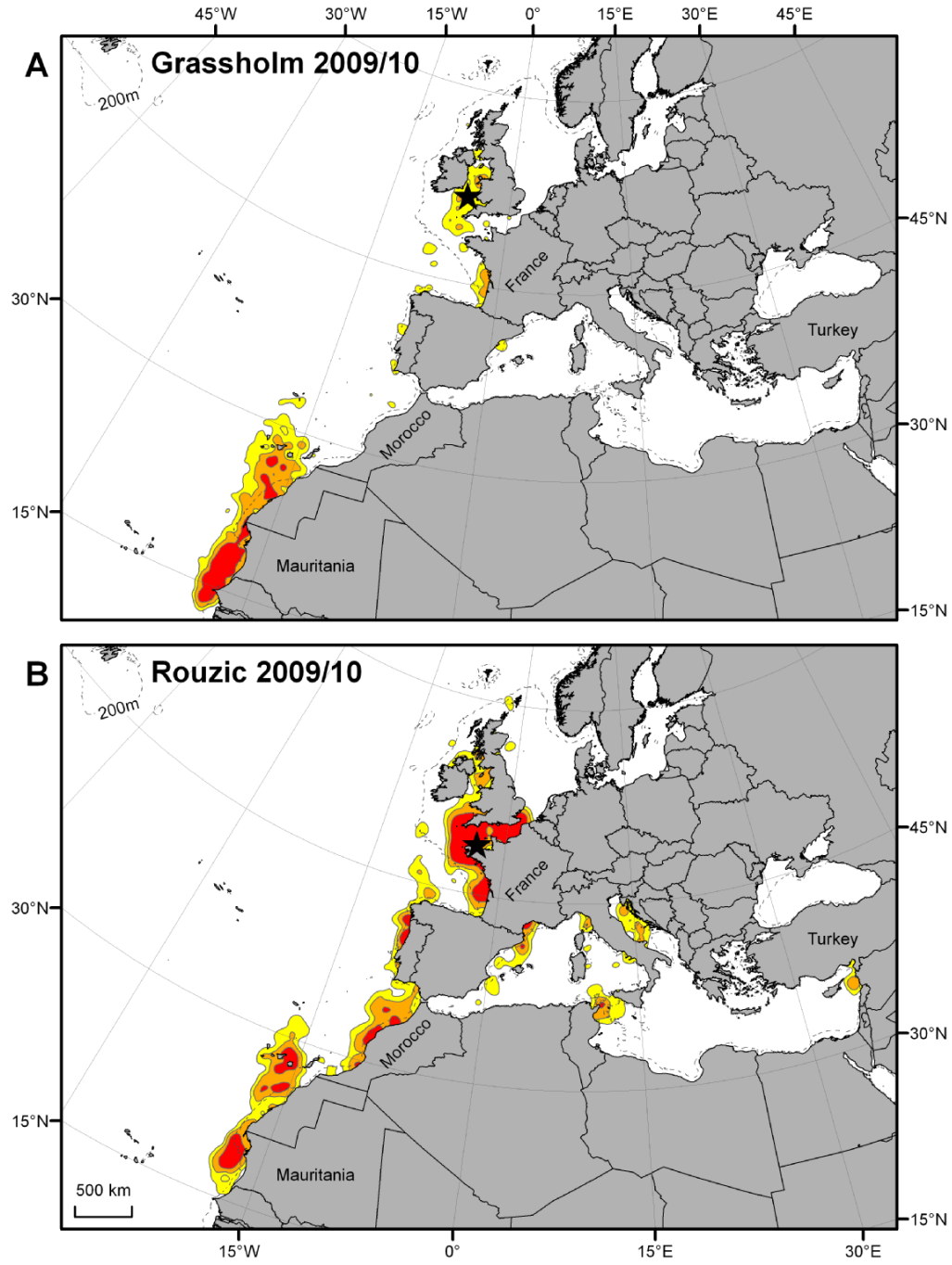

Figure 4.1 The over-winter distributions (kernel density contours) of northern gannets tracked from two colonies: Grassholm, UK (A, n = 13) and Rouzic, France (B, n = 21). Colours represent 25% (red), 50% (orange) and 75% (yellow) contours for all fixes (Grassholm n = 2564, Rouzic n = 3511) recorded during the winter period October 2009 to January 2010. Breeding colonies are indicated with a star, dotted line indicates position of continental shelf (200 m bathymetric line).

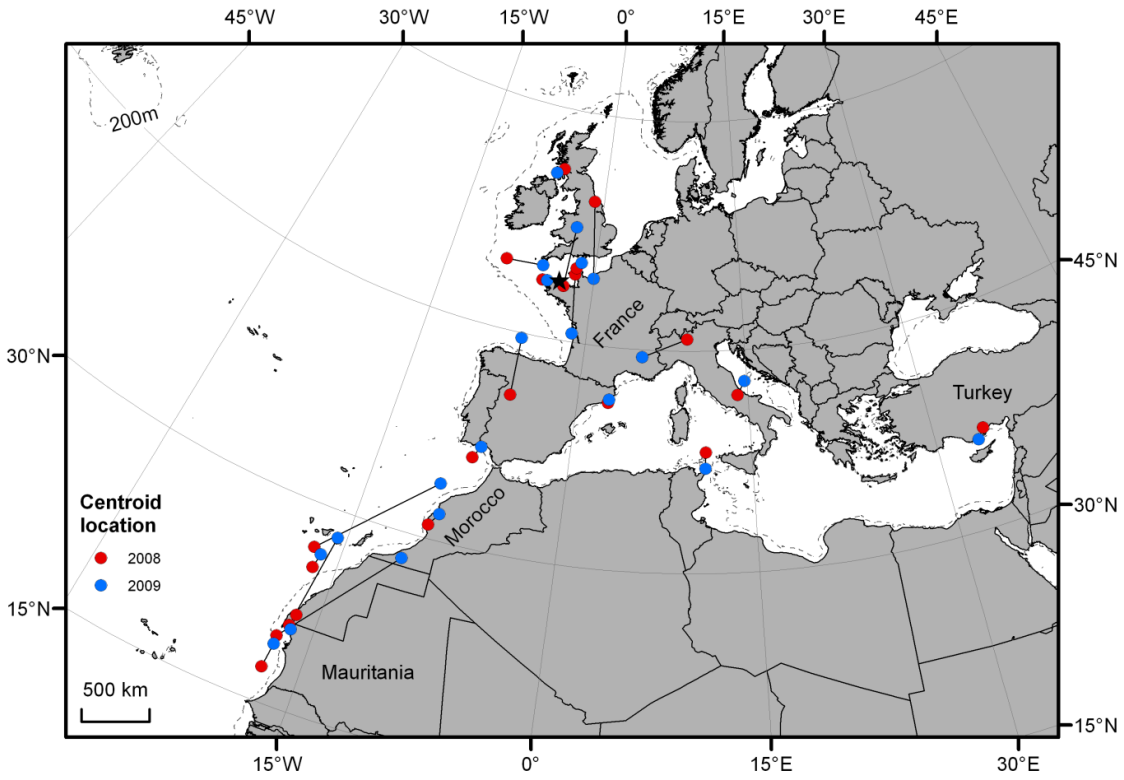

Figure 4.2 Individual northern gannets show high over-wintering site fidelity, circles indicate the centroid winter location for each individual tracked from Rouzic, France during 2008/2009 (red) and 2009/2010 (blue) with connecting lines indicating movement between seasons. The Rouzic breeding colony is indicated with a star, dotted line indicates position of continental shelf (200 m bathymetric line).

Winter foraging consistency

There was a high degree of repeatability between-years in the isotopic signatures of primary feathers sampled from individuals breeding on Grassholm, for both $\delta^{13}C$ ($r = 0.733 \pm 0.149$, $n = 13$, $p = 0.001$, Figure 4.4A) and $\delta^{15}N$ ($r = 0.609 \pm 0.184$, $n = 13$, $p = 0.011$, Figure 4.4B). Isotope ratios in body feathers were also repeatable between years, for both $\delta^{13}C$ ($r = 0.848 \pm 0.097$, $n = 13$, $p < 0.001$, Figure 4.4C) and $\delta^{15}N$ ($r = 0.657 \pm 0.176$, $n = 13$, $p = 0.008$, Figure 4.4D). Given that individuals winter in similar locations, isotopic repeatability would suggest that individuals also feed on prey with the same isotopic signature in multiple years.

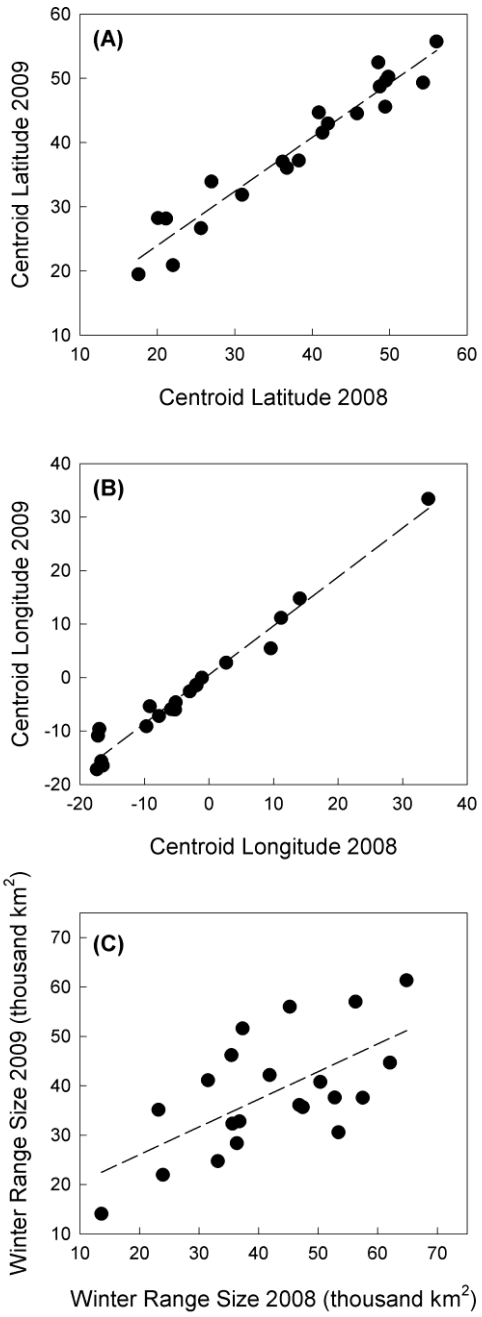

Figure 4.3 Individuals tracked over two successive over-wintering periods reveal a high degree of repeatability in both centroid latitude (A) and longitude (B), and over-wintering range size (C).

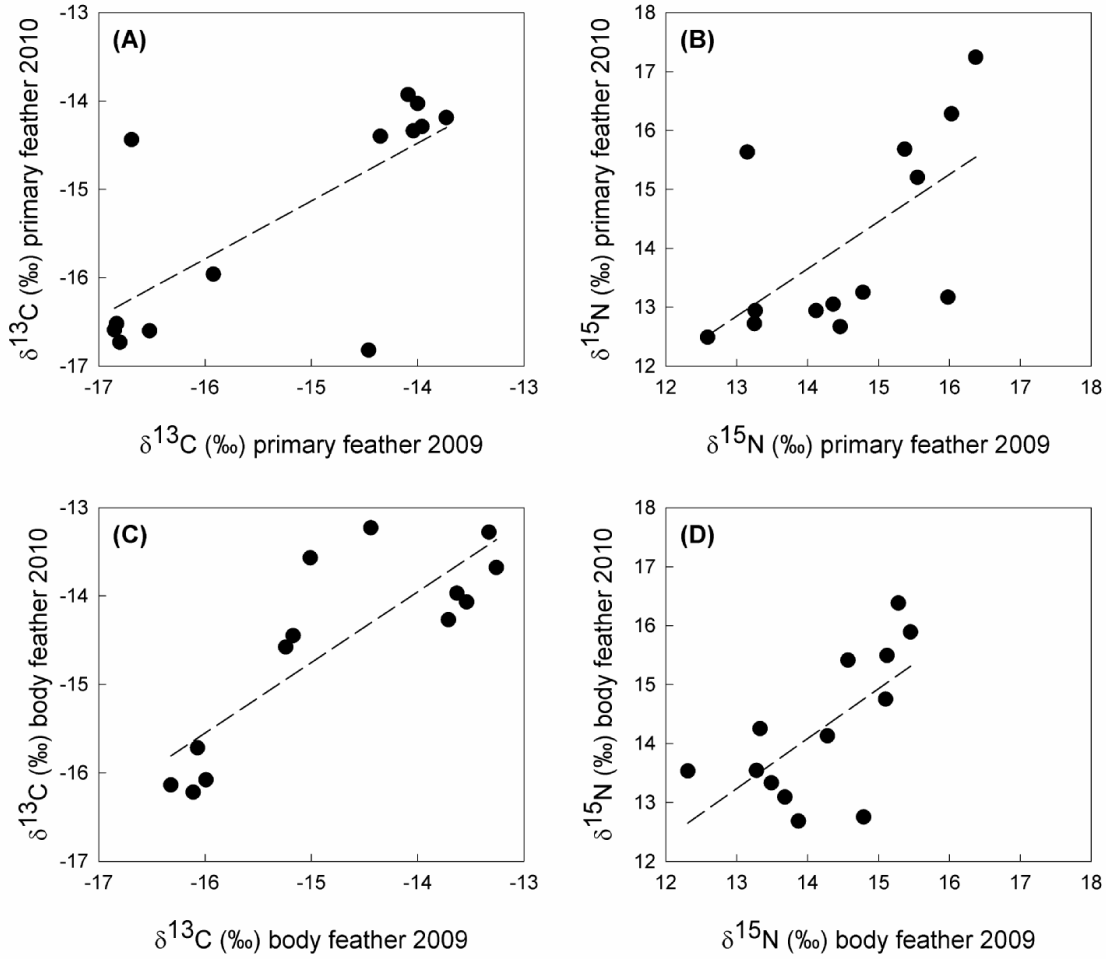

Figure 4.4 The stable isotope signatures of individuals sampled in successive years show repeatability in both carbon (A) and nitrogen (B) of primary feathers, and the carbon (C) and nitrogen (D) of body feathers, suggesting inter-annual consistency in foraging strategy.

Combining geolocation and isotopic information

We discriminated between the effects of foraging location and prey type on the isotopic signature of individual birds by testing for isotopic differences between wintering areas. Ratios of $\delta^{13}C$ and $\delta^{15}N$ in winter-grown primary feathers of individuals from Rouzic showed no segregation by wintering strategy (MANOVA: Pillai = 0.366, $F_{4, 34} = 1.907$, $p = 0.132$, Figure 4.5A). By comparison, individuals from Grassholm showed a degree of isotopic segregation by wintering strategy (MANOVA: Pillai = 1.156, $F_{4, 20} = 6.847$, $p = 0.001$, Figure 4.5B). Post-hoc analyses showed this difference to be in $\delta^{13}C$ ($F_{2, 10}$ =

7.746, $p = 0.009$) and not $\delta^{15}N$ ($F_{2, 10} = 1.990$, $p = 0.187$). Therefore, as variability in $\delta^{15}N$ does not appear to be an effect of wintering region, the observed repeatability in $\delta^{15}N$ may instead reflect individual variation in trophic level that persists across years.

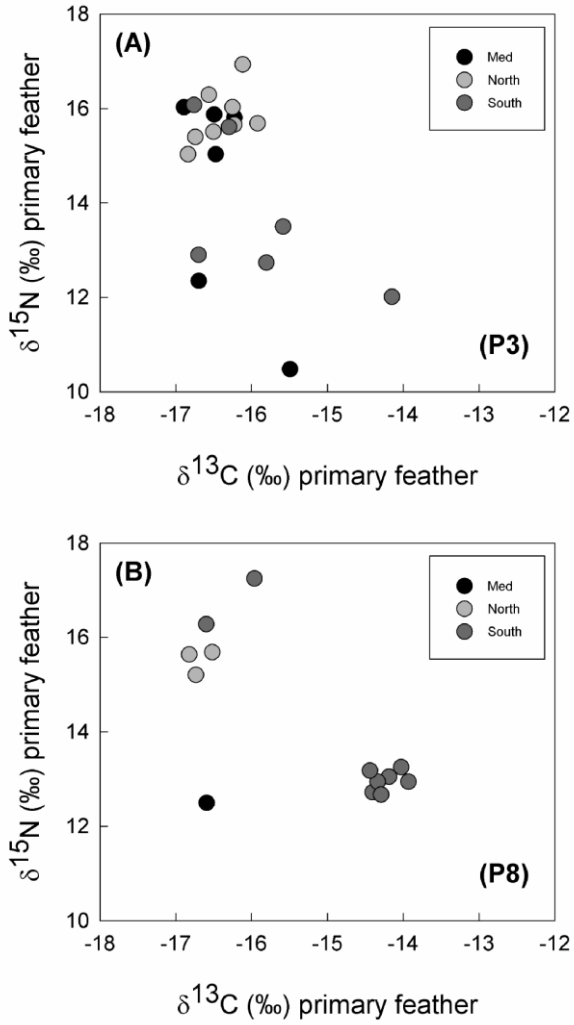

Figure 4.5 Comparison of the ratios of stable carbon and nitrogen isotopes in winter grown primary feathers with over-wintering strategies determined by geolocation of individuals tracked from Rouzic (A) and Grassholm (B), reveals variation both within and between over-wintering location.

Carry-over effects

Date of arrival at the colony was positively correlated with migration distance (GLMM $\chi^2_1 = 6.152$, $p = 0.013$, Nagelkerke $R^2 = 0.29$) and differed between colonies, with individuals from Rouzic arriving an estimated 12.6 ± 3.6 days earlier than

individuals returning to Grassholm (χ^2_1 = 10.366, p = 0.001, Figure 4.6). There was no correlation between date of arrival and δ^{15}N in winter grown primary feathers for individuals returning to either Rouzic ($F_{1, 10}$ = 1.093, p = 0.320), or Grassholm ($F_{1, 9}$ = 0.238, p = 0.637).

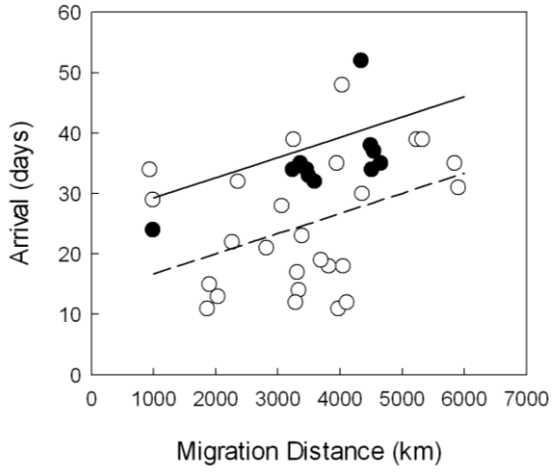

Figure 4.6 Carry-over effects of migration distance on chronology. Timing of arrival (days from 1st January) at the colony was positively correlated with migration distance (GLMM χ^2_1 = 6.152, p = 0.013, Nagelkerke R^2 = 0.288) and differed between colonies, with individuals from Rouzic (hollow circles, dashed line) arriving an estimated 12.6 ± 3.6 days earlier than individuals returning to Grassholm (filled circles, solid line) (χ^2_1 = 10.366, p = 0.001).

BMI was significantly correlated with migration distance, and the slope of this relationship differed significantly between colonies ($F_{1, 28}$ = 11.897, p = 0.002, R^2 = 0.33, Figure 4.7). Separate analysis of the colonies revealed a significant negative correlation between BMI and migration distance for individuals from Rouzic ($F_{1, 18}$ = 4.888, p = 0.040, R^2 = 0.54), and a significant positive correlation between BMI and migration distance for individuals from Grassholm ($F_{1, 10}$ = 11.897, p = 0.006, R^2 = 0.21). There was no correlation between BMI and δ^{15}N in winter grown primary

feathers for individuals returning to either Rouzic ($F_{1, 17} = 1.466$, $p = 0.243$), or Grassholm ($F_{1, 10} = 1.900$, $p = 0.198$).

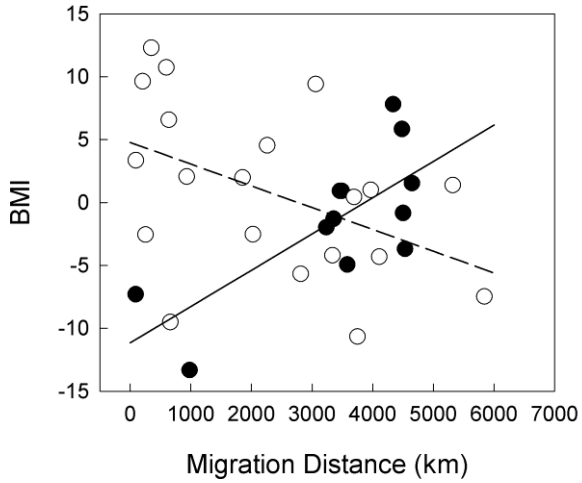

Figure 4.7 BMI was significantly correlated with migration distance, and differed between colonies ($F_{1, 28} = 11.897$, $p = 0.002$, $R^2 = 0.329$). The BMI of individuals from Rouzic (hollow circles and dashed line) was negatively correlated with migration distance ($F_{1, 18} = 4.888$, $p = 0.040$, $R^2 = 0.543$), while the BMI of individuals from Grassholm (filled circles and solid line) was significantly positively correlated with migration distance ($F_{1, 10} = 11.897$, $p = 0.006$, $R^2 = 0.214$).

4.4 DISCUSSION

Here we document a rare example of both winter philopatry and foraging consistencies impacting fitness proxies in an apex marine predator. Individual gannets returned to the same region and occupied ranges of similar sizes in consecutive winters (Figure 4.2 and 4.3) and analysis of winter-grown primary feathers sampled in successive years revealed a high degree of individual repeatability in stable isotope ratios (Figure 4.4). Without sampling the prey base of gannets across the wintering grounds it is not possible to infer individual preference in prey type, but combining isotopic and positional information can separate the effects of foraging location and prey on feather isotope ratios. This revealed population level variation within wintering location (Figure 4.5), and indicates that the observed isotopic repeatability was not due solely to

wintering location, but that individual variation in trophic level (inferred from $\delta^{15}N$) within the wintering locations may persist across years. There were also consequences for different wintering strategies: timing of arrival at the colony was positively correlated with migration distance (Figure 4.6), and BMI was correlated with migration distance, but differed between colonies (Figure 4.7). We discuss these findings below.

Combining geolocation and isotopic information

Both winter site fidelity and the repeatability of tissue isotope signatures have been reported in a wide range of taxa before (e.g. Phillips et al., 2005b, Broderick et al., 2007, Woo et al., 2008, Hjernquist et al., 2009). Nevertheless, while repeatability in an isotopic signature may suggest that individuals feed on prey with the same isotopic signature in multiple years, without information on the location of wintering sites it has previously been difficult to discriminate the causes of isotopic repeatability (Hjernquist et al., 2009). Individuals may 1) winter in the same location and forage on the same prey in successive years, or 2) may winter in different locations and forage on different prey in successive years, but this results in the same isotopic signature. By combining information on the winter location of an individual with isotopic information from winter-grown primary feathers we were able to tease apart two potential mechanisms. The isotopic signatures of individuals showed variation both within and between wintering areas, suggesting the adoption of a range of different foraging strategies (Figure 4.5). Moreover, the observed repeatability in isotopic signatures indicates that these strategies may persist across years. This variation within wintering area suggests that it may not always be appropriate to use stable isotopes to assign winter quarters, and highlights the need to approach isotopic assignment with caution.

Consequences and potential mechanisms of individual specialisation

Recent empirical evidence has shown that gannets exhibit individual foraging specialisations during the breeding season (Votier et al., 2010), and our findings build on this, providing evidence for consistent individual differences in foraging and wintering behaviour during the non-breeding period. The isotopic signatures of primary feathers grown on the West African wintering grounds by individuals from Grassholm differed by up to ~3‰ in $\delta^{15}N$ and ~2 ‰ $\delta^{13}C$ (Figure 4.5B). This difference in $\delta^{15}N$ equates to approximately one trophic level and could be due to individuals targeting discarded demersal white fish rather than shoaling pelagic species such as mackerel *Trachurus spp*., pilchard *Sardina spp*., or anchovy *Engraulis spp*. The difference in $\delta^{13}C$ could be due to individuals adopting offshore rather than inshore foraging strategies (Hobson et al., 1994, Votier et al., 2010). The consistency in isotopic signatures from repeat sampling individuals suggests these differences persist across years. Estimates of individual range sizes are potentially inflated for birds that travel further from the colony because of the reduced reliability of light-based latitude estimates closer to the equator. However, when migration distance was included as a covariate in a GLM, its effect was not significant ($F_{1, 18} = 0.734$, $p = 0.403$) and range size in winter 2008 remained a significant predictor of range size in 2009 ($F_{1, 19} = 12.861$, $p = 0.002$, $R^2 = 0.40$).

A potential mechanism for the persistence of between-individual differences may be resource competition during the non-breeding period, and consistent individual differences in habitat preference and foraging behaviour could mediate intra-specific resource partitioning (Hyrenbach et al., 2002, Phillips et al., 2005a, Phillips et al., 2005b). Niche partitioning has been reported for a wide range of species during the winter period (Phillips et al., 2009, Young et al., 2010) and if it were to prove

advantageous would likely persist over multiple seasons, so becoming further canalised (Dall et al., 2004). As generalist marine predators, gannets potentially compete for food with a number of other species at the wintering grounds and dispersal across a wide-range of locations may allow individuals to reduce both intra- and inter-specific competition, as is seen in a number of species during the non-breeding period (Nicholls et al., 2002, Phillips et al., 2005b, Witt et al., 2011). If competition was high, then individuals may be expected to become highly specialised to reduce niche and spatial overlap, or equally individuals may become generalists, operating in broader niches and ranging over larger areas. It is likely that these strategies are not mutually exclusive, but instead frequency dependent (Bergmüller and Taborsky, 2010, Pires et al., 2011).

Migratory strategies may be heritable, or be the result of cultural transmission (Møller, 2001, Bêty et al., 2004), but little is known of the genetic component to over-wintering behaviour, although studies of passerines suggest it may be large (Berthold and Helbig, 1992). However, individuals of long-lived species may also accumulate knowledge of suitable winter foraging areas, allowing some flexibility in over-wintering location dependent on local environmental conditions (Phillips et al., 2005b). Breeding constraints may also cause changes to migratory strategy, and there is evidence of age structuring in winter distributions (Marques et al., 2010). Repeatability may therefore be life stage dependent (Bolnick et al., 2003, Bergmüller and Taborsky, 2010) and higher when measured over short timeframes (Bell et al., 2009), or it may be a transitory phenomenon (Catry et al., 1999); further work is required.

Carry-over effects

There were a number of consequences of winter behaviour, and patterns differed between colonies. Migration distance was positively correlated with arrival date and so

those birds wintering closer to the colony returned earlier. Reproductive success correlates with time of arrival at the breeding grounds (Bêty et al., 2004), early arriving individuals may benefit through earlier access to higher-quality territories (Marra et al., 1998), and laying late has been associated with fledging fewer young in gannets (Nelson, 2002). Individuals arrived at Rouzic an estimated 12.6 days earlier than those returning to Grassholm, and bred earlier. Gannet phenology is known to correlate with latitude, but our observed difference is larger than the 5.6 day difference in lay date that might be predicted by the 1.98 day advancement per 1° latitude described by Wanless et al. (2008).

The BMI of individuals returning to Rouzic was negatively correlated with migration distance, and so individuals that wintered near the colony returned in better condition than those wintering further away. Maximum migration distance is a compromise between the fitness benefits and costs associated with migrant versus resident strategies (Møller, 2001). Therefore, for the Rouzic population, the adoption of a resident strategy may avoid the costs associated with a lengthy migration, allowing the allocation of more resources to the breeding event. For individuals returning to Grassholm, BMI was positively correlated with migration distance. It is unclear what direction carry-over effects may take (Harrison et al., 2010), and the optimum migratory strategy for the Grassholm population may differ from the Rouzic population, i.e. high quality individuals from Rouzic may wintering close to the colony, while high quality individuals from Grassholm winter in West Africa. There are large water mass and food web differences between the three wintering areas utilised by gannets, and individuals from Grassholm may be better able to utilise the highly productive waters off the West African coast.

Nevertheless, this colony difference may also be due to the leverage of two northern migrants that returned to the colony in poor body condition. The body measurements and tissue isotope ratios of these two males are not outside the range of measurements taken from other individuals from Grassholm, so this difference is unlikely to be a due to nutritional or sex effects. However, due to the small sample size we treat this colony difference with caution. Furthermore, individuals from Rouzic were sampled up to two months earlier than those breeding on Grassholm and differences may be due to sampling at different stages in the breeding season. Positional information also indicates that individuals return to the colonies from January onwards, and so body condition measures were sampled 5-6 months after they first arrived at the breeding grounds. Our measure of body condition, recorded during chick rearing, may therefore also integrate a measure of the costs of reproduction rather than be a carry-over effect (Bogdanova et al., 2011). We are also unable to distinguish between the cause and effect of intrinsic quality. Condition may not be an effect of the winter location, rather poor quality individuals may be outcompeted near the colony by better quality individuals and so be forced to winter further from the colony. We found no correlation between winter grown primary feather $\delta^{15}N$ and either timing of arrival at the colony or BMI. Carry-over effects will most likely be a function of both location and diet during the winter period; however, here we do not have enough statistical power to investigate foraging strategy differences within wintering location.

Conservation implication

The waters around the UK, Ireland and France hold 70% of the world breeding population of northern gannets (Mitchell et al., 2004) and so successful protection is of paramount importance to European conservation efforts. While the breeding grounds are adequately protected, there is currently no legislation in place to protect wintering

habitats, in which mature birds spend between 3-4 months of the year (2008/9, 105 ± 11 days, n = 9; 2009/10, 97 ±15 days, n = 22) and juveniles may spend a great deal longer (Marques et al., 2010). The conservation implications of a wide ranging population are complex, but extreme wintering site fidelity may allow particular priority areas to be targeted; for example, where birds are known to overlap with specific threats such as fisheries bycatch (Lewison et al., 2004a), or offshore development (Inger et al., 2009, Grecian et al., 2010).

Conclusion

We conclude that gannets adopt individual migratory and foraging specialisations that persist over multiple years, potentially allowing individuals to repeatedly target heterogeneously distributed food resources during winter, and that these strategies have consequences for individual condition and phenology. These patterns may arise to reduce competition for resources such as food and space during the non-breeding period, or be the result of heritable migratory traits.

Chapter 5:
The Northwest African upwelling region as a hotspot for wintering marine vertebrates and commercial fisheries: Troubled waters ahead?

Abstract

Upwelling zones are globally important drivers of marine ecosystems and crucial biodiversity hotspots, supporting large communities of fish and a wide-range of apex predators, that either breed adjacent to these regions in huge colonies or migrate many thousand kilometres to utilise these areas in the non-breeding period. However, these areas face unprecedented levels of anthropogenic-driven pressures from offshore development, pollution, climatic change and commercial fisheries. The non-breeding period is a vital element of the annual cycle, and so understanding the interactions between marine vertebrates and these threats at wintering grounds is paramount to conservation efforts. I collate information on the distributions of five different species of apex predator wintering in the Northwest African upwelling region, report the on-going long-term increase in landings of pelagic fish in this region and highlight the need for pelagic marine protected areas to adequately protect migratory animals throughout the annual cycle. It is likely that large populations of marine predators and massive fisheries exploitation in this region are mutually exclusive in the long-term.

5.1 INTRODUCTION

The global importance of upwelling regions

Upwelling zones are globally important drivers of marine ecosystems, cycling nutrient rich cold water into the photic zone and stimulating primary productivity. This in turn feeds food-webs, drives bottom-up trophic forcing and results in upwelling zones being among the most productive regions on the planet. There are five major coastal upwelling regions; the Canary Current, Northwest Africa; the Benguela Current, Southern Africa; the California Current, western North America; the Humboldt Current, western South America; and the Somali Current, East Africa. These areas are crucial biodiversity hotspots, supporting large communities of fish and a wide-range of apex predators, that either breed adjacent to these regions in huge colonies (Weichler et al., 2004, Grémillet et al., 2008a, Pichegru et al., 2009), or migrate many thousand kilometres to utilise these areas in the non-breeding period (Hyrenbach et al., 2006, Petersen et al., 2008, Peron et al., 2010, Witt et al., 2011 and Chapter 4).

Threats to the marine environment

Upwelling regions, along with other sections of the marine environment, face an unprecedented level of anthropogenic-driven pressures. Among the main threats are offshore development (Gill, 2005, Inger et al., 2009, Grecian et al., 2010), pollution (Islam and Tanaka, 2004, Votier et al., 2005, Votier et al., 2008b), climatic change (IPCC, 2001, Pounds and Puschendorf, 2004, Thomas et al., 2004, Harley et al., 2006), and commercial fisheries (Pauly et al., 1998, Worm et al., 2009). For coastal upwelling regions, foremost amongst these threats is over fishing because, while they represent < 1% of the world's oceans by area, they provide ~20% of global catch (Pauly and Christensen, 1995). Furthermore, studies have shown that species relying on upwelling

regions during the breeding season are unable to adapt to ecosystem level changes caused by over-fishing (Pichegru et al., 2010b).

Current global fishing practices have a wide range of impacts, including the removal of top-predators from coastal and pelagic ecosystems; the targeting of fish further down marine food webs resulting in a net decrease in trophic levels; the depletion of global fish stocks; the bycatch of non-target species; and the recent escalation of illegal, unreported and unregulated (IUU) fisheries (Pauly et al., 1998, Pauly et al., 2002, Myers and Worm, 2003, Lewison et al., 2004a, Worm et al., 2009). Fisheries compete with marine vertebrates for fish, but may also provide increased food resources through the provision of offal and discards (Arcos and Oro, 2002, Votier et al., 2004b); the annual global estimate for discarded species is 8% of catch, or 7.3 million tonnes per year (Kelleher, 2004). The consequences of increased fishing effort for marine vertebrates are complex; for example, the removal of predatory fish may also lead to trophic cascades that increase numbers of prey species (Furness, 2003).

Protecting the marine environment

Conservation measures have begun in some upwelling regions, for example in the California Current (Hyrenbach et al., 2006), Benguela Current (Pichegru et al., 2010a), and Humboldt Current (Awkerman et al., 2005). In Northwest Africa, the Canary Current passes along the Banc d'Arguin coastline of Mauritania, a UNESCO World Heritage Site protecting a migration flyway for an estimated 7 million migrant waders, the world's largest concentration of wintering shorebirds (IUCN, 1989), and one of the last viable remnant populations of the Mediterranean monk seal *Monachus monachus* a critically endangered pinniped, and one of the most endangered mammals (IUCN, 2011). Nevertheless, the collapse of several major fisheries in the 1990s has led to a

global shift of fishing effort toward Africa (Worm et al., 2009). The Northwest African upwelling region, comprising the seasonal Moroccan and Senegalese upwellings and the permanent Mauritanian upwelling produced by the Canaries Current, has now become one of the most intensively fished areas on the planet (Laurans et al., 2004, Lewison et al., 2004b, Zeeberg et al., 2006, Worm et al., 2009). Expansion of the Northwest African fishery has been linked to changes in the trophic structure of the marine ecosystem (Laurans et al., 2004), and depleted stocks could lead to encroachment of the Banc d'Arguin, protection of which only extends up to 60 km offshore (IUCN, 1989). Therefore, quantifying the usage of this area by both marine vertebrates and fisheries, and the potential damage being caused to the ecosystem, is a conservation priority.

Tracking the movements of marine vertebrates

Marine vertebrates, such as seabirds, cetaceans, sea turtles and some fish, are top-predators in marine ecosystems and are capable of travelling large distances to target seasonally productive regions. Three species of interest are the northern gannet *Morus bassanus*, the *graellsii* subspecies of lesser black-backed gull *Larus fuscus graellsii*, and the great skua *Stercorarius skua*. The UK and Ireland between them support an estimated 60-70% of the global populations of each. Two other species of interest are the Cory's shearwater *Calonectris diomedea*, and loggerhead turtle *Caretta caretta*; these species are known to use major coastal upwelling regions and are both vulnerable to pelagic longline fisheries (Cooper et al., 2003, Lewison et al., 2004b, Hawkes et al., 2006, González-Solís et al., 2007). Recent telemetry and band recovery analysis suggests that all five of these species may use the Northwest African upwelling region for at least part of the non-breeding period (Furness et al., 2006, Hawkes et al., 2006, González-Solís et al., 2007, Kubetzki et al., 2009, Marques et al., 2010, Dias et al., 2011).

Understanding the interactions between marine vertebrates and fisheries requires detailed information on individual movements, but this has historically been difficult to obtain. Mark/ recapture studies provide information on the location and status of marked individuals (Hestbeck et al., 1991, Berthold, 2001, Wernham et al., 2002, Godley et al., 2003), and ringing data exist over large timescales allowing examination of potential historical trends in distribution (Wernham et al., 2002, Clark et al., 2009), or age effects (Marques et al., 2010). Nevertheless, these data may be biased by spatio-temporal variation in band recovery (Mehl et al., 2004) or band effects (Broderick and Godley, 1999, Saraux et al., 2011). Recently, the development of bio-logging technology (reviewed by Ropert-Coudert et al., 2009) has proven vital in expanding our understanding of migratory species, e.g. seabirds (Phillips et al., 2005b), sea turtles (Witt et al., 2011), cetaceans (Baumgartner and Mate, 2005), sharks (Jorgensen et al., 2010), fish (Block et al., 2005), and pinnipeds (Bradshaw et al., 2004), and has allowed interactions between seabirds and fishing vessels to be examined in near real-time (Bartumeus et al., 2010, Votier et al., 2010, Granadeiro et al., 2011, Torres et al., 2011).

Importance of the non-breeding period

Bio-logging studies have characterised the long-distance migrations of a number of marine vertebrates that move between specific breeding and wintering grounds (Block et al., 2005, Phillips et al., 2005b, Witt et al., 2011). These studies have also revealed the importance of particular migratory fly-ways, staging and stop-over areas (Shaffer et al., 2006, Guilford et al., 2009). In many instances, conservation efforts aimed at protecting marine vertebrates tend to be focused at either the breeding grounds (Reid and Webb, 2005, Wanless et al., 2007, Bicknell et al., 2009, Witt et al., 2009), or the near colony areas used for maintenance behaviours during the breeding season (McSorley et al., 2003, McSorley et al., 2008, Wilson et al., 2009). However, the

breeding season represents only a small proportion of the annual cycle, and it is now clear that migratory fly-ways, staging areas and wintering grounds should also form part of an integrated approach to conserving biodiversity (SEO/BirdLife, 2009, BirdLife, 2010b). The non-breeding period allows individuals to recover from previous breeding attempts, accumulate resources before the next breeding event (Barbraud and Weimerskirch, 2005), and the conditions experienced during this period may interact with events in the other (Daunt et al., 2006, Harrison et al., 2010 and Chapter 4). Moreover, the majority of mortality occurs during the winter period (Barbraud and Weimerskirch, 2003). Nevertheless, despite accumulated evidence that wintering grounds and migration routes are of major importance during the annual cycle of marine vertebrates, they are afforded little protection, especially when compared with breeding locations. Wintering areas may be large, bisected by national borders, or occur in international waters, and so implementing protection in these regions is problematic (Hyrenbach et al., 2000, Shillinger et al., 2008). Globally, protection is lacking and the total proportion of the world's oceans currently designated as Marine Protected Areas (MPAs) is between 0.08% and 0.65% (Wood et al., 2008).

Data requirements

Pelagic or high seas MPAs could provide useful tools in marine conservation, but there are concerns over the types of data required to aid their design and implementation (Game et al., 2009, Kaplan et al., 2010, and Chapter 3). Nonetheless, there are a number of large-scale datasets available that could provide a convenient baseline for designation purposes; (1) Remotely-sensed sea-surface temperature or sea-surface chlorophyll data provide proxies for ocean productivity; (2) telemetry data can provide information on individual level habitat utilisation; (3) mark-recapture data provides information on historical trends in distributions; and (4) fisheries landings data provide

coarse scale information on fisheries pressure and a proxy for fish distributions. Data on the distribution of fisheries could also be taken from Vessel Monitoring Systems (VMS), but this data is not readily available (Witt and Godley, 2007). The combination of these data streams could provide an integrated approach to pelagic MPA designation.

Here, we collate information on remotely sensed environmental variables to characterise the Northwest African upwelling zone. We then combine information on the post-breeding movements of four apex predators; three seabird and one sea turtle species, comparing habitat utilisation during the non-breeding period with spatially resolved information on fisheries landings from the Northern and Eastern Atlantic.
We then examine historical trends by comparing wintering movements of UK seabirds with decadal locations of ring recoveries and temporal patterns in fisheries landings. We use this information to highlight the importance of the Northwest African upwelling system, and highlight the need to designate pelagic MPAs to prevent the inevitable collision between the requirements of increased fisheries exploitation and the needs of marine vertebrates.

5.2 METHODS

Describing the marine environment

To characterise marine productivity and provide a proxy of suitable foraging locations for marine vertebrates we extracted global 9 km^2 resolution winter seasonal climatology composites (21 December to 20 March) of sea surface temperature (SST, °C) and chlorophyll *a* distribution (mg m^{-3}) for the period 2002-2010, from the MODIS instrument on board the Aqua (EOS PM) satellite (http://oceancolor.gsfc.nasa.gov/). We also use information on the location of ocean currents adapted from Pinet (2006).

Tracking marine vertebrates through the non-breeding period

In June 2008, we deployed 40 mk7 British Antarctic Survey (BAS) geolocation sensors (GLS) on adult northern gannets breeding at Rouzic, France (48.900°N, 3.436°W) a colony of circa 17,500 breeding pairs (Grémillet et al., 2006). In July 2009 we deployed 20 mk5 BAS GLS on adults breeding at Grassholm, Wales (51.730°N, 5.486°W) a colony with circa 39,000 breeding pairs (Murray, 2009). Birds were selected at random, away from the edge of the colony, and caught under appropriate regional licences using either a brass noose or crook, attached to the end of a pole. In June 2009 we deployed 20 mk5 BAS GLS on adult lesser black-backed gulls breeding at Gugh on the Isles of Scilly, UK (49.891°N, 6.330°W), a colony of circa 250 breeding pairs. Birds were selected at random, across three sub-sites within the main colony, and caught under licence using a radio controlled noose trap placed around the nest cup during incubation and camouflaged with a thin layer of grass. Loggers were attached to a plastic ring using two cable ties and fitted to the tarsus. The total device mass did not exceed 10g, representing < 0.4% of adult gannet body mass, and < 1.6% of adult lesser black-backed gull body mass. During 2010, 21 loggers (52.5%) were retrieved from Rouzic, 13 (65%) from Grassholm, and 7 (35%) from Gugh.

Positional information was calculated from GLS data following standard methods (Wilson et al., 1992, Phillips et al., 2004). Briefly, geolocation relies on estimating the timings of sunset and sunrise using set thresholds in the light curves recorded by the logger. Latitude can be derived from day length, and longitude from the timing of local midday and midnight, with respect to Greenwich Mean Time and Julian day, providing two positions per day with an accuracy of circa 186 ± 114 km (Phillips et al., 2004). However, around the vernal and autumnal equinoxes day and night are of equal length, and so it becomes impossible to estimate latitude.

Light curves recorded by tags retrieved from lesser black-backed gulls and gannets were analysed using BAS TransEdit and BirdTracker software. On the basis of calibration data from fixed points, and knowledge of likely wintering areas relative to land masses, a threshold of 10 and an elevation angle of -4.0° were used for processing files, with the exception of those from two loggers in which the epoxy had clouded by the time of retrieval, for which an elevation angle of -3.5° was deemed to be more appropriate. We removed obviously erroneous locations associated with interference in light curves around the time of sunset and sunrise. Location errors can occur through shading of the tag and during equinox periods. All positions recorded up to 10 days either side of the equinox were removed, as well as any fix obviously affected within four weeks of the equinox. Filtering removed 33.8 ± 7.4% of fixes. Validated data were smoothed twice to reduce the error associated with geolocation (Phillips et al., 2004).

A 500 km boundary from the colony was used to separate the breeding and wintering periods (sensu Guilford et al., 2009) as this represents the maximum foraging extent of birds during chick rearing (Votier et al., 2010). Departure and arrival were designated as the occurrence of two or more positions outside or inside the 500 km boundary, those individuals never consistently more than 500 km from the colony were assigned as resident. In order to map distributions of resident individuals and those that crossed this boundary during the equinox, the winter period was defined as the average departure and arrival days for the migratory population.

Tracking additional species

In 2004 and 2005, ten satellite transmitters were attached to post-nesting female loggerhead turtles (see Hawkes et al., 2006). Estimates of animal movements relayed by the Argos system (CLS, France) are provided with an estimate of location error

(location class, LC). Data were filtered to provide one fix of Location Class (LC) 3, 2, 1, 0, or A per day (Witt et al., 2010). When more than one position of LC 3 (accuracy > 250 m) was available we selected a position randomly to limit temporal bias in satellite pass frequency. Information on the non-breeding movements of 30 adult Cory's shearwaters tracked from four colonies between 2000 and 2005 using geolocation sensors was extracted from the Birdlife International Global Procellariiform Tracking Database (González-Solís et al., 2007, BirdLife, 2010a).

Assessing temporal trends in species distributions using ring recovery information

Historical patterns in the distribution of three long-distance migrants from the UK and known to rely on fisheries discards; gannets, lesser black-backed gulls, and great skuas were inferred from the British Trust for Ornithology (BTO) ring recovery database, which collates information on the location of recovered and re-sighted individually marked birds. We filtered recoveries reported between 1971 and 2010 following Wernham et al. (2002) using the following filters; (1) Date of recovery accurate to within 15 days; (2) Finding co-ordinate accurate to within 1 degree of latitude; (3) Exclude recoveries reported as moved before finding (but include those moved by water); (4) Exclude birds ringed and transported before release; (5) Exclude birds ringed and held for 24 hours before release. We aged birds by adding the estimated age at ringing to the time difference between ringing and recovery, and considered gannets aged 5+ years, lesser black-backed gulls (4+ years), and great skua (7+ years) as adults (Wernham et al., 2002). We also only considered recoveries reported during the winter period as defined by Wernham et al. (2002): gannets (1st December – 28th February) , lesser black-backed gulls (15th November – 28th February), and great skua (15th November – 14th March).

Information on the spatio-temporal distribution of fisheries

Spatially resolved fisheries data are available through the United Nations Food and Agricultural Organisation (FAO). We use total annual landings (live weight equivalent in tonnes) for two major FAO areas, the Northern European waters managed by the International Council for the Exploration of the Sea (ICES) and the West African waters managed by the Fishery Committee for the Eastern Central Atlantic (CECAF). This provides information on fisheries resources across the northeast and eastern central Atlantic, key areas for wintering aggregations of a number of marine vertebrate species. Data were available from 1970 to 2008 for CECAF (FAO, 2010a) and 1950 to 2009 for ICES (FAO, 2010b) via Fishstat Plus, grouped according to International Standard Statistical Classification of Aquatic Animals and Plants (ISSCAAP). Annual landings data were filtered to include demersal and pelagic fish from the following ISSCAPP species groups (FAO codes are shown in brackets): Shads (24); Flounders, halibuts, soles (31); Cods, hakes, haddocks (32); Miscellaneous coastal fishes (33); Miscellaneous demersal fishes (34); Herrings, sardines, anchovies (35); Tunas, bonitos, billfishes (36); Miscellaneous pelagic fishes (37); Marine fishes not identified (39). Individual fish species, or species groups were then assigned as either demersal (including bentho-pelagic species) or pelagic using FishBase (Froese and Pauly, 2011), we excluded two ambiguous groups (Finfishes, and Marine fishes). Not all landings data are provided with an accurate location and may straddle current ICES borders; these were removed from our analysis of spatial fish distributions along with catch data that did not fit with the current boundary classification of ICES and CECAF divisions. Trawl fisheries for demersal finfish and shrimp are estimated to account for over 50% of all discards, while representing approximately 22% of total landings (Kelleher, 2004). Demersal landings therefore provide a good representation of regional discarding rates, while also supplying a food resource otherwise unavailable to seabirds (Votier et

al., 2004b). We present spatially resolved data for ICES and CECAF statistical girds, using the most recent landings information, 2009 for ICES and 2008 for CECAF. We present temporal trends in landings data by plotting annual recorded landings per km^2 for the duration of the respective datasets; 1950 to 2009 for ICES, and 1970 to 2008 for CECAF.

Statistical analysis

Prior to interpretation, and to allow comparison across datasets, we binned all positional information (tracks and ring recoveries) into 200 km x 200 km grid squares, which is approximately equal to the error associated with geolocation (Phillips et al., 2004), using an European Albers equal-area conic projection. To test for temporal changes in the use of the Northwest African upwelling region we compared the number of recoveries below the 36°N meridian, and 6°W parallel for each decade using Chi-squared tests. We present positional and ring recovery information as percentages to allow comparison across data sets. Fisheries landings were corrected for the size of statistical area to allow comparison between regions. All analyses were carried out in ArcGIS 9.3 (ESRI, USA), MATLAB R2009b (The Mathworks, USA), and R 2.11.1 (R Development Core Team, Austria).

5.3 RESULTS

Describing the marine environment

The Northwest coast of Africa is subject to persistent northerly winds, causing a year round upwelling which is drawn offshore by the southward moving Canary Current (Figure 5.1A). The continental shelf is close inshore and shelves steeply, constructing a strong inshore temperature gradient that wraps around Cap Blanc in Mauritania; there is an average 6°C winter temperature gradient between Cape Verde and the Cap Blanc

(Figure 5.1B). This upwelling, and the convergence of a number of currents in this region, provides the nutrients to feed very high density blooms of chlorophyll *a* (Figure 5.1C). The upwelling zone expands south in the winter, reaching circa 5°N in January-March, then retreats during the summer to a minimum extent of 15°N (Heileman and Tandstad, 2011).

Tracking marine vertebrates through the non-breeding period

During the 2009/10 winter period gannets were widely distributed across the North Sea, Mediterranean, and Northwest African upwelling region (Figure 5.2A, and Chapter 4). Centres of distribution focused around the south west of the UK, Bay of Biscay, and 47.1% of all tracked birds wintered along the Moroccan, Mauritanian, and Senegalese coastlines. The wintering distribution of lesser black-backed gulls focused around the English Channel, Bay of Biscay, Iberian Peninsula, and 57.1% of all tracked birds wintered along the Moroccan and Senegalese coasts (Figure 5.2B). Cory's shearwaters have a very broad non-breeding distribution and are known to conduct pan-Atlantic migrations (González-Solís et al., 2007), nevertheless one key area highlighted here is the Mauritanian coast (Figure 5.2C). All tracked loggerhead turtles moved east of the Cape Verde Islands (Hawkes et al., 2006); seven individuals spent the non-breeding period in the oceanic waters between Cape Verde and the West African coast, while three individuals moved south east down the West African coastline to the inshore waters off Guinea and Sierra Leone (Figure 5.2D).

Spatial distribution of fisheries landings

Analysis of the most recently available FAO data (FAO, 2010a, FAO, 2010b) revealed that vessels across European and West African waters recorded large landings of pelagic fish in 2009 and 2008 respectively, up to 2.5 tonnes km^{-2} in the North Sea,

Baltic Sea, western Irish waters and across Moroccan and Western Saharan coasts (Figure 5.3A). Demersal landings were much lower, generally up to 0.15 tonnes km^{-2}, but were higher (up to 2.5 tonnes km^{-2}) around Norway and Iceland (Figure 5.3B). Demersal fleets are known to produce high levels of discards, and so this difference suggests European waters potentially offer a larger source of discarded fish when compared with West African landings.

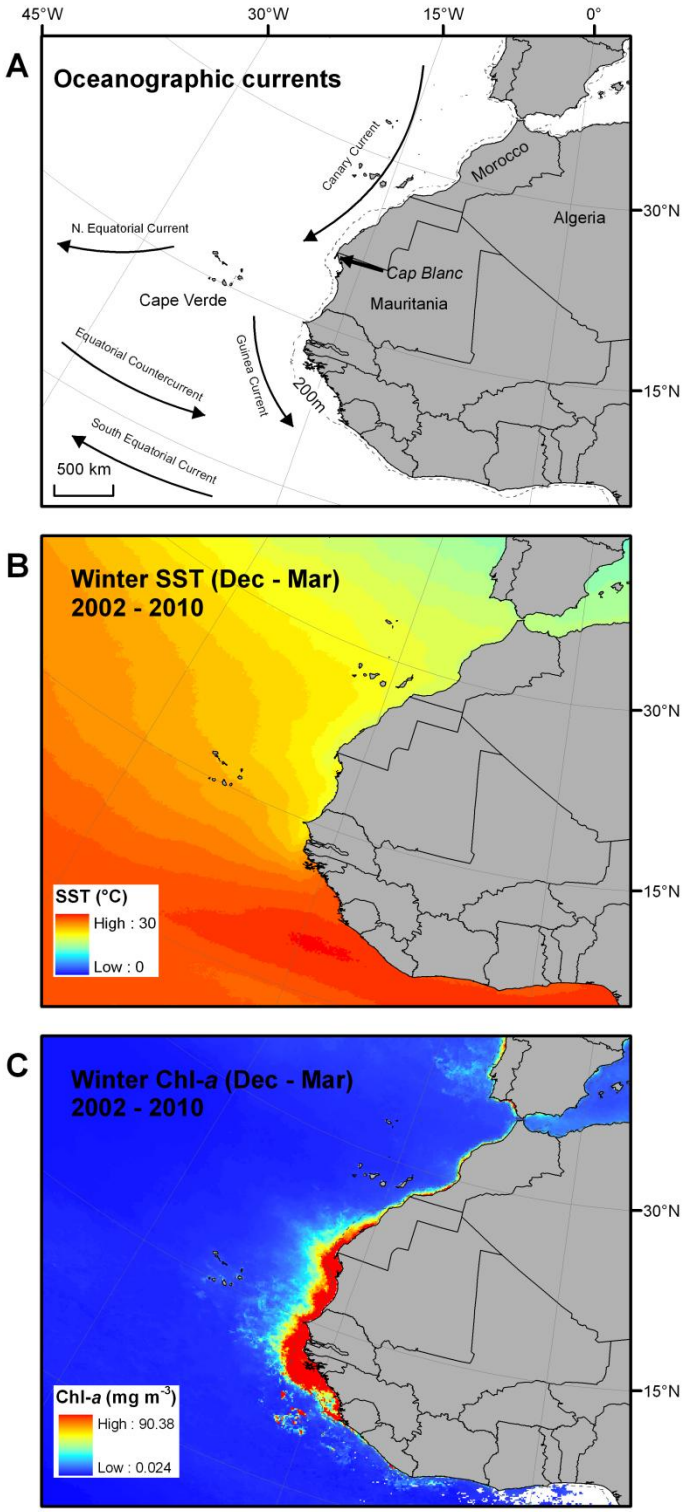

Figure 5.1 Characterising the Northwest African upwelling zone, (A) the location of key oceanographic currents, (B) average winter sea surface temperature gradient, and (C) the average winter abundance of Chlorophyll *a*.

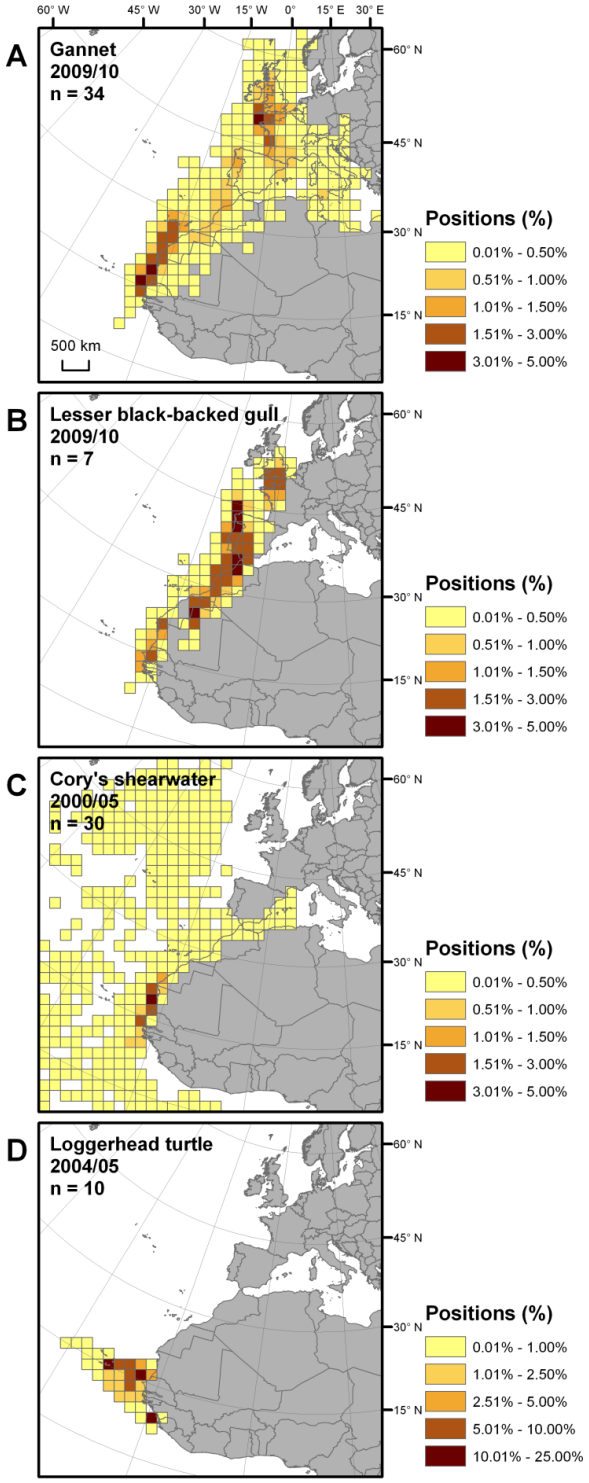

Figure 5.2 Distribution of geolocator and satellite positions from three species of seabirds, and one species of sea turtle that winter in the Northwest African upwelling region. Data represent one fix per individual per day summed into 200 km x 200 km grid squares and displayed as a percentage of the total number of fixes for that species.

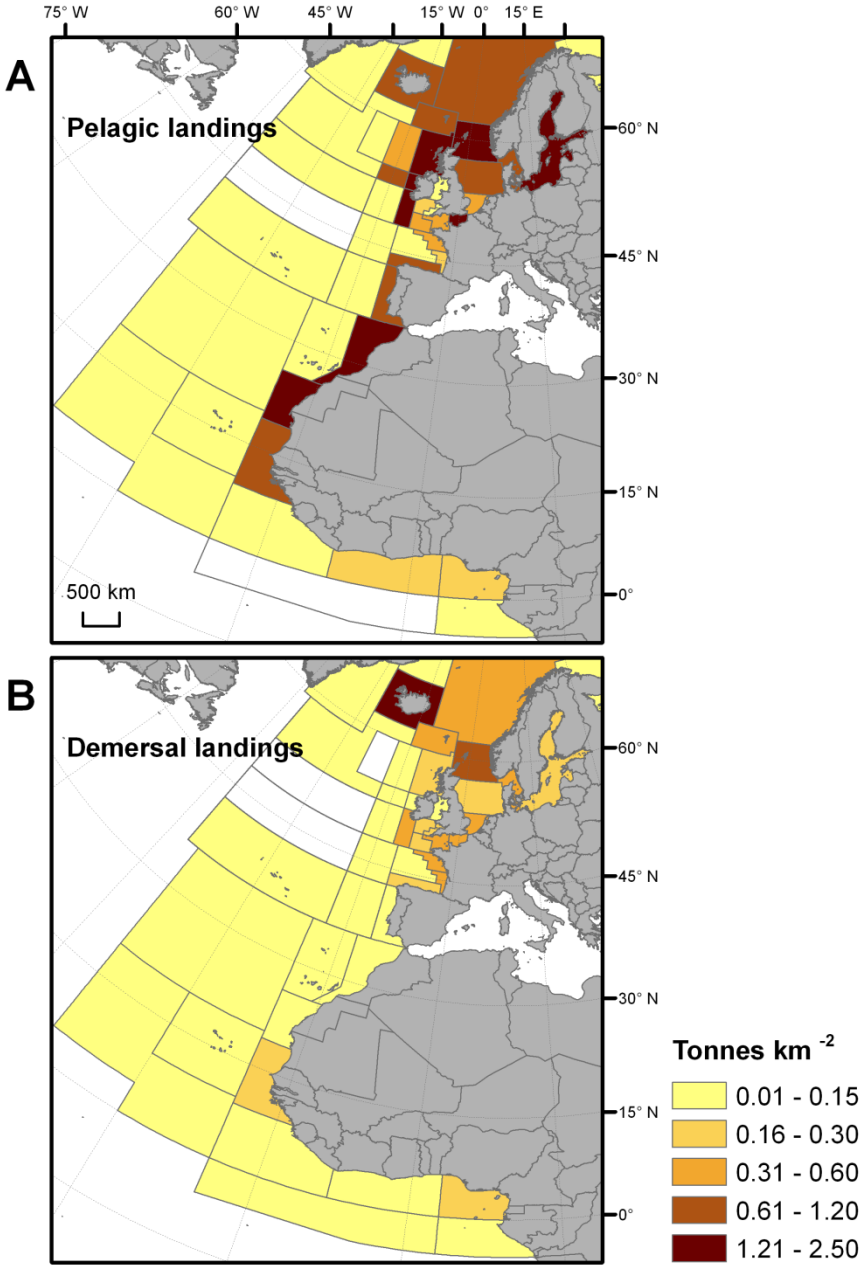

Figure 5.3 Spatial distribution of the most recent reported total annual landings for ICES (2009) and CECAF (2008) statistical grids. Landings data were split into (A) pelagic and (B) demersal groups (see methods), and presented as tonnes landed (wet weight equivalent) per km^2.

Assessing temporal trends in species distributions using ring recovery information

Mapping forty years of ring recovery data from gannets produced centres of distribution in the south west UK, English Channel, southern North Sea and Bay of Biscay, and few ring recoveries on the coast of Morocco, Western Sahara and Senegal (Figure 5.4). Reports of lesser black-backed gulls are much more widespread, with centres of distribution further south and along the Iberian Peninsula (Figure 5.5). The majority of great skua recoveries are from the coast of the European mainland, from Norway to the Iberian Peninsula (Figure 5.5). We further explored these patterns by splitting the data by decade and age class. Immature gannets (aged up to 4 years) tended to show a wider distribution than adults (aged 5 years or more) but this difference was not significant ($\chi^2_6 = 8.000$, $p = 0.238$). There was no temporal pattern in the reporting of recoveries to suggest a shift in wintering distribution for either adult ($\chi^2_3 = 1.571$, $p = 0.666$) or immature gannets ($\chi^2_3 = 7.714$, $p = 0.052$). There was no difference in the distribution of reported recoveries between adult and immature lesser black-backed gulls ($\chi^2_9 = 12.000$, $p = 0.213$). However, the reported recoveries of both adult ($\chi^2_3 = 293.286$, $p < 0.001$), and immature birds ($\chi^2_3 = 356.695$, $p < 0.001$) differed between decades, showing a southerly expansion, from circa 30°N in the 1970s to circa 15°N in the 1990s and 2000s (Figure 5.5). Recoveries of immature great skuas (aged less than 7 years) were more widely distributed than adults (aged 7 or more years) during in the 1970s and 1980s (Figure 5.6), but recoveries overall showed no difference ($\chi^2_4 = 5.000$, $p = 0.287$). There was no temporal difference in the recovery of adult great skuas ($\chi^2_3 = 2.000$, $p = 0.572$), and as nine of the ten immature great skuas recovered below 36°N were recovered between 1971 and 1980 we were unable to test for temporal effects across decades

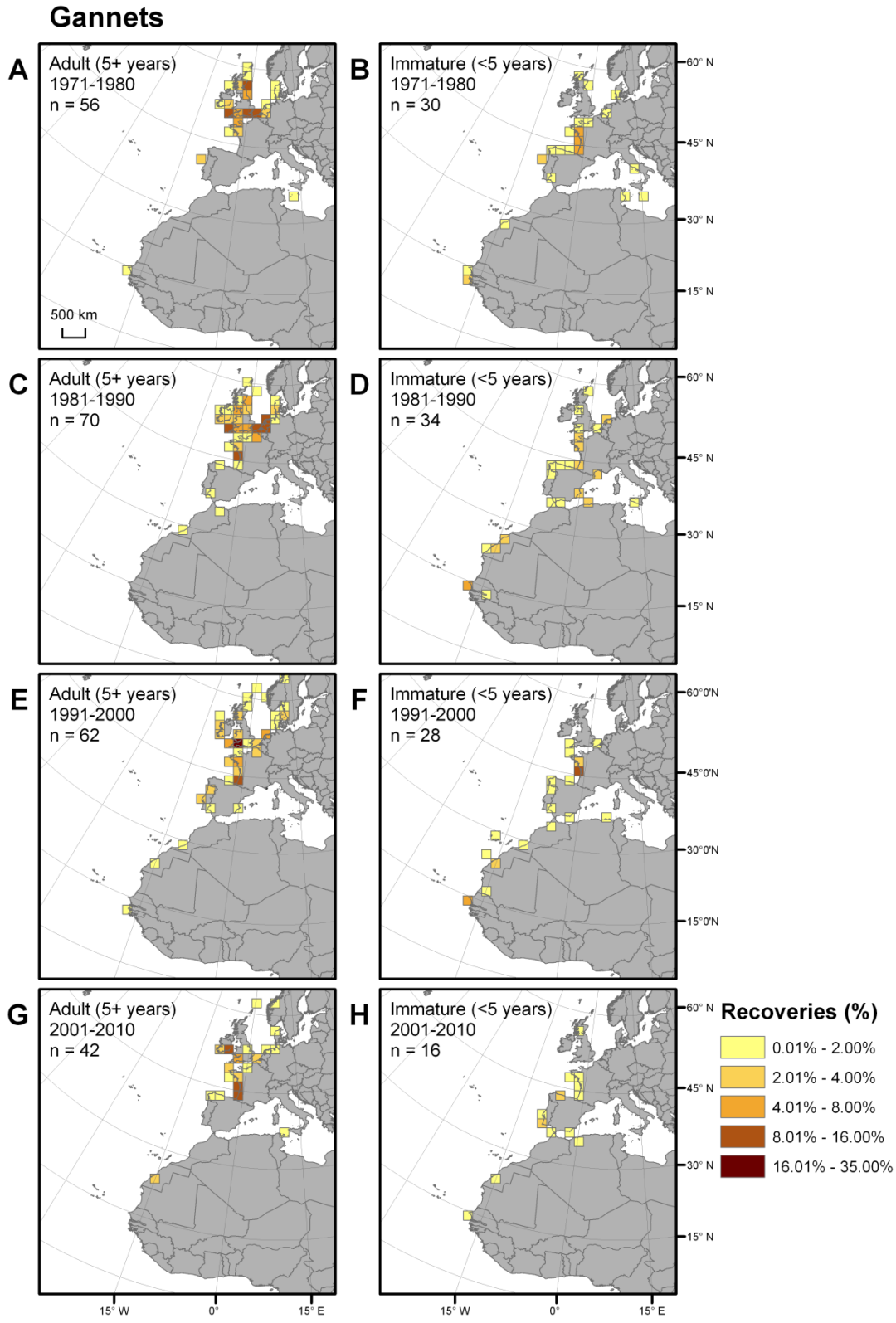

Figure 5.4 The reported location of winter ring recoveries from gannets originating from UK colonies, split by age (left-right) and decade (top-bottom). Recoveries are summed into 200 km x 200 km grid squares and presented as a percentage of the total number of recoveries per group.

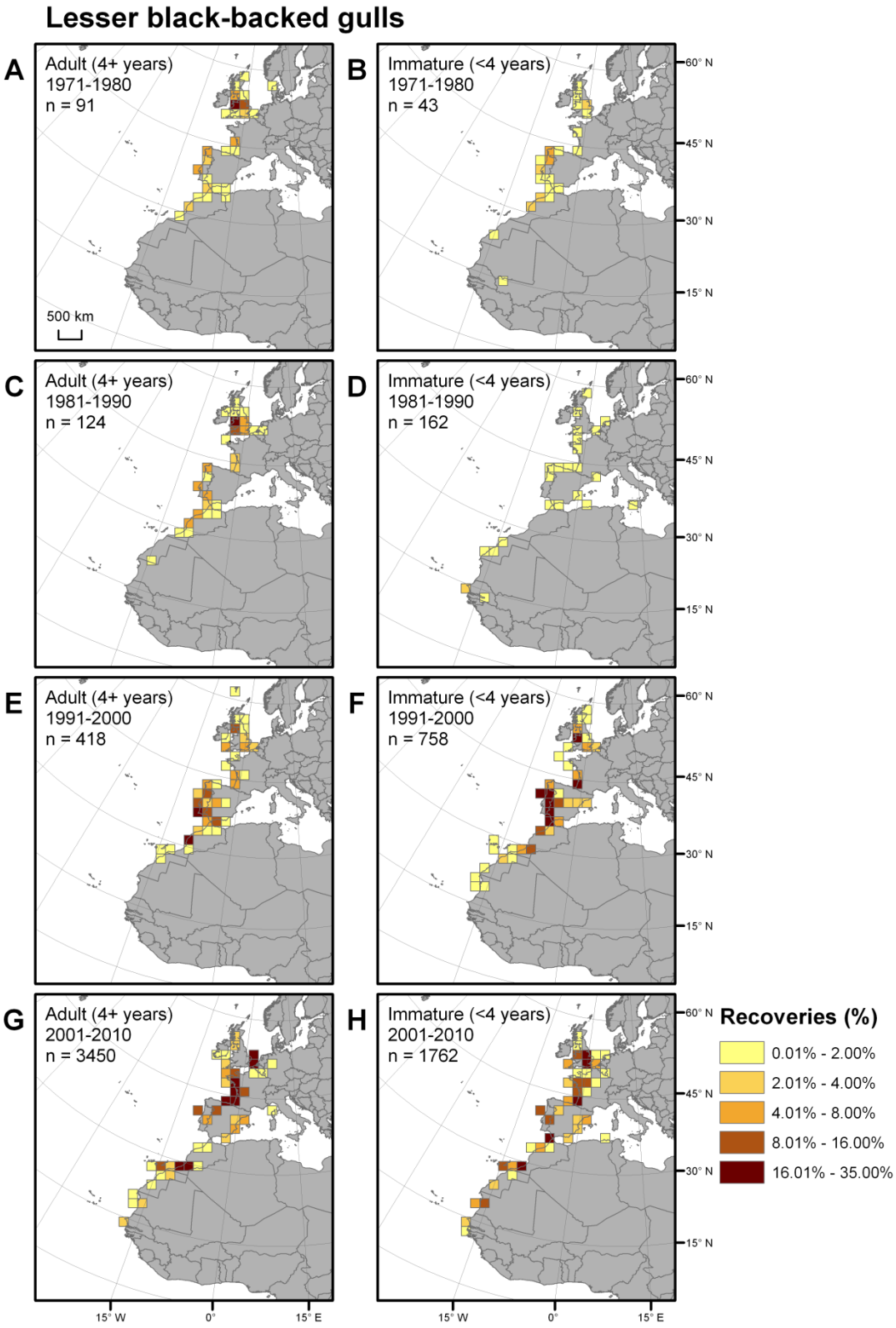

Figure 5.5 The reported location of winter ring recoveries from lesser black-backed gulls originating from UK colonies, split by age (left-right) and decade (top-bottom). Recoveries are summed into 200 km x 200 km grid squares and presented as a percentage of the total number of recoveries per group.

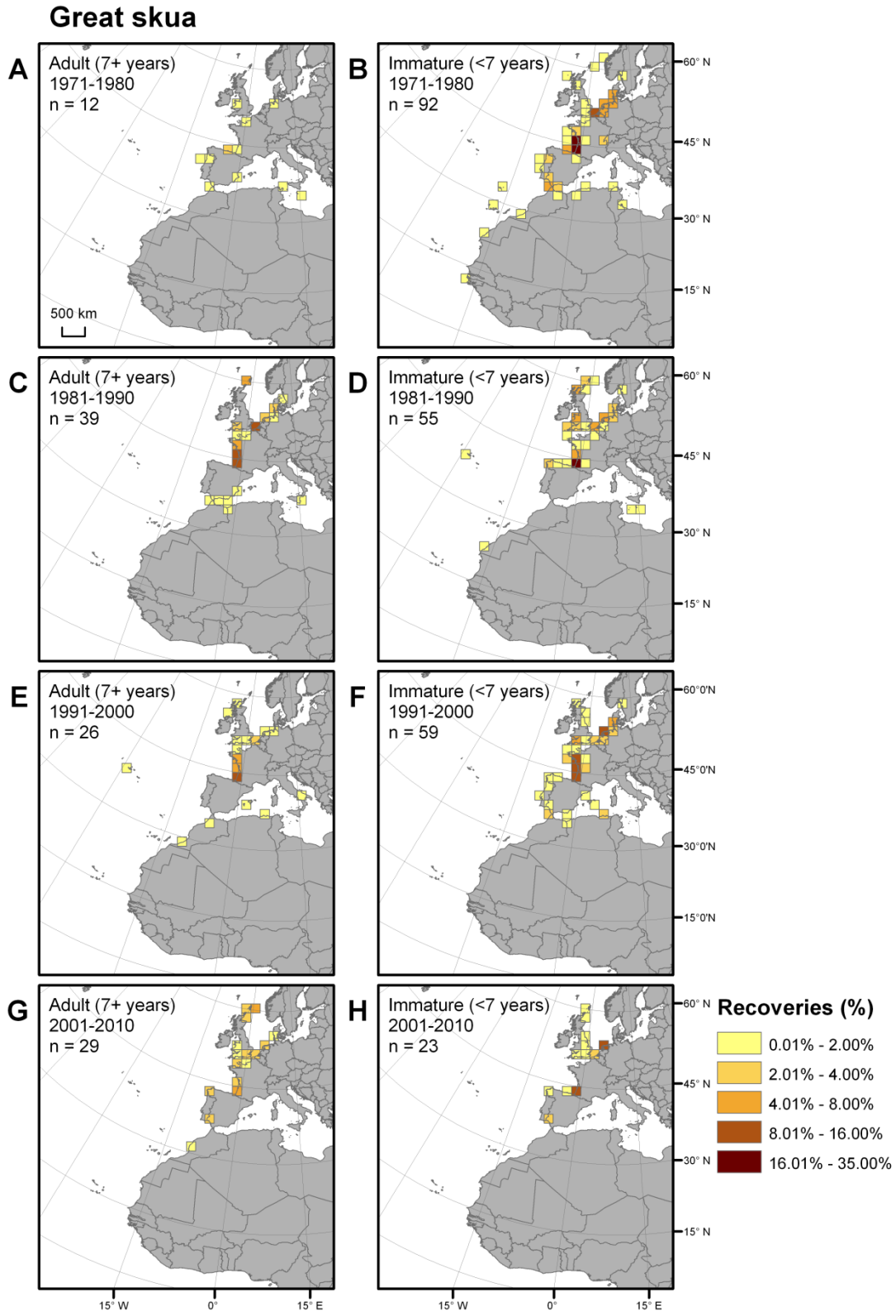

Figure 5.6 The reported location of winter ring recoveries from great skua originating from UK colonies, split by age (left-right) and decade (top-bottom). Recoveries are summed into 200 km x 200 km grid squares and presented as a percentage of the total number of recoveries per group.

Assessing temporal trends in fishery landing data

Fishery landings within ICES squares peaked in the mid-1970s and have declined in recent years, while CECAF landings have remained relatively stable (Figure 5.7A). Separating these data into demersal and pelagic classes reveals a slow decline in demersal landings from within the ICES divisions while CECAF landings are lower but much less variable (Figure 5.7B). There has been a general increase in the pelagic landings within both ICES and CECAF divisions since the 1970s (Figure 5.7C), but ICES pelagic landings have declined since the early 2000s.

Few tracked marine vertebrates utilised waters in northern ICES areas or were found far offshore (Figures 5.2 and 5.4-7), therefore we also compare landings excluding far northern waters (above circa 60°N) and the open ocean (beyond circa 20°W). These show a similar pattern to the large scale data. Northern European landings have seen a general decrease since 1970, while West African demersal landings remain constant (Figure 5.8A). Landings of pelagic species in both areas fluctuate over time but show a steady increase, Northern European landings of pelagic species have recently declined from mid-2000 levels (Figure 5.8B).

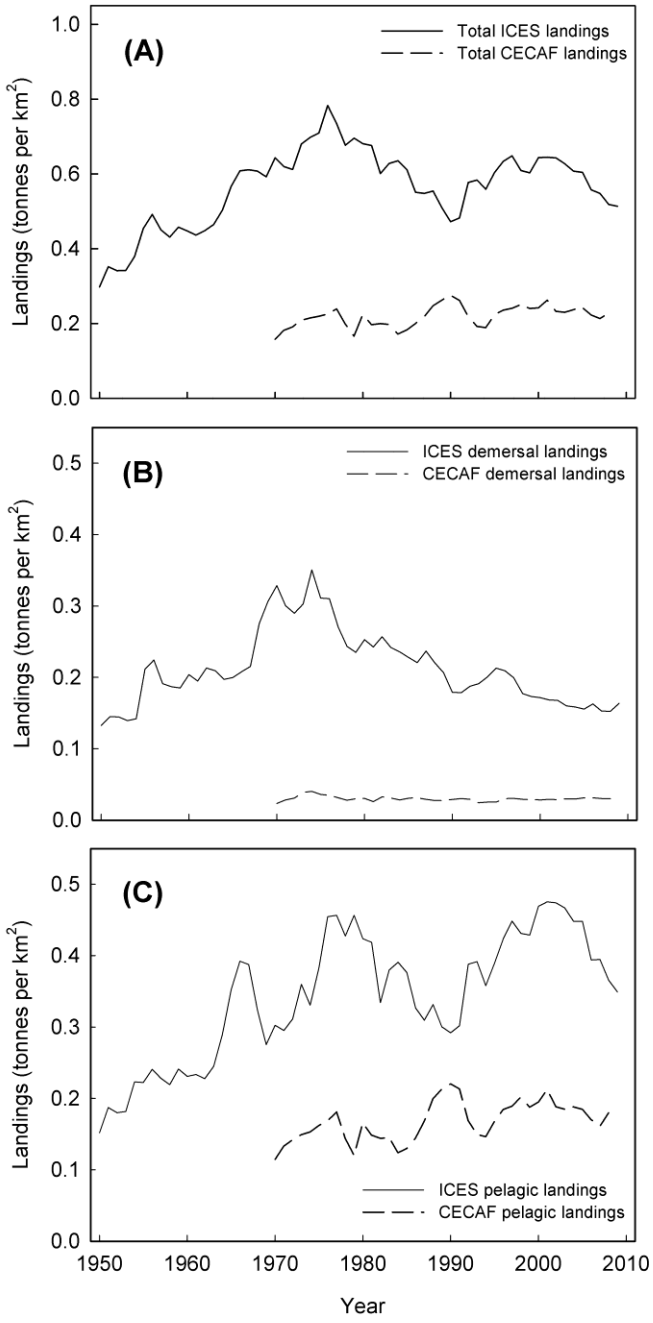

Figure 5.7 Temporal patterns in the reported total annual landings (A) of fish caught in ICES (1950 – 2009) and CECAF (1970 – 2008) divisions, and comparison of the relative contribution of (B) demersal and (C) pelagic groups (for classification see methods).

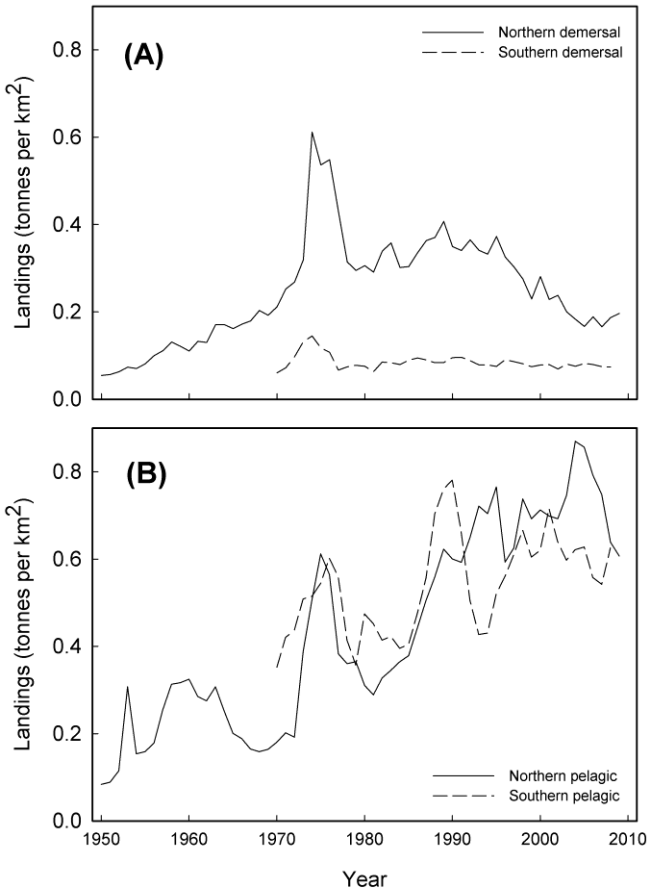

Figure 5.8 Temporal patterns in the reported total annual landings of (A) demersal and (B) pelagic fish for FAO divisions utilised by marine vertebrates between 1971 and 2010. FAO divisions were separated to include only those areas highlighted by either tracking or ring recovery data.

5.4 DISCUSSION

Here, we show that a range of important seabird species and one sea turtle species utilise the Northwest African upwelling region during the non-breeding period. Analysis of temporal sightings data suggest this region may have been utilised by UK originating seabirds for a number of decades. Furthermore, we report the on-going long-term increase in landings of pelagic fish in this region. It is likely that large populations of marine predators and intense fisheries exploitation in this region are mutually exclusive in the long-term.

Over-winter distributions

The species tracked in this study were widely distributed during the non-breeding period, and all utilised the Northwest African upwelling region for at least part of the winter period (Figure 5.2). Interestingly, the spatial distributions of gannets and lesser black-backed gulls tracked from UK colonies differed from the locations of forty years of ring recovery information. There are two hypotheses that may explain this; that (1) a lack of observers on the west coast of Africa prevents rings from being recovered, or that (2) due to changes in environmental factors over the last forty years the winter ranges of a number of migrant species have expanded further south. Splitting the ring recovery data by decade and age class suggests a southern expansion for lesser black-backed gulls but not gannets or great skuas. However, lesser black-backed gull populations in northern Europe are now subject to an intensive mark/ recapture program. Winter recoveries have increased from 134 individuals in the 1970's to 5212 individuals in the 2000's, and so this southern expansion could be due to an increase in ringing and resighting effort (Figure 5.5). By comparison recoveries of ringed gannets and great skua have remained low throughout this period (Figures 5.4 and 5.6). The reported recoveries of gannet and great skua are much lower than those for lesser black-backed gulls and so, while immature birds tended to be more widely distributed than adults, we could detect no temporal trend in the data. This suggests that the numbers of seabirds wintering in the Northwest African upwelling region have not increased over the last 40 years, but that detectability and recovery in this region is very low.

The Northwest African upwelling region is known to be important for wintering aggregations of a wide range of other marine vertebrates including; Ocean sunfish *Mola mola* (Sims et al., 2009); long-tailed skuas *Stercorarius longicaudus* (Sittler et al., 2011), pomarine skuas *Stercorarius pomarinus* (Camphuysen and van der Meer, 2005),

Cape Verde shearwaters *Calonectris edwardsii* (Newell et al., 1997), black terns *Chlidonias niger* (Van der Winden, 2002), grey phalaropes *Phalaropus fulicarius* (Camphuysen and van der Meer, 2005), Sabine's gulls *Xema sabini* (Newell et al., 1997, Camphuysen and van der Meer, 2005), and southern hemisphere migrant south polar skuas *Stercorarius maccormicki* (Newell et al., 1997).

Fisheries discards as a food source

Previous work suggests that a number of seabird species may be targeting the large fishing fleets that trawl the productive Mauritanian shelf waters (Camphuysen and van der Meer, 2005, Furness et al., 2006), and discards from demersal vessels are known to provide a resource that would otherwise be unavailable to seabirds (Votier et al., 2004b). There is evidence that gulls, skuas and gannets facultatively target discarding fleets during the breeding season (Furness et al., 1992, Votier et al., 2010), and stable isotope analysis of winter-grown primary feathers suggest the same may be true during the winter period (see Chapter 4). However, demersal landings have decreased in European waters over the last forty years, thus reducing the potential discarding resource. The impact of this change on seabird populations could be mitigated if seabirds were to target fleets further south, but the CECAF demersal fleet is much smaller than the ICES fleet, and the overall discarding rate for CECAF (10.5%) lower than that of ICES (13.0%) (Kelleher, 2004).

It is unlikely, therefore, that seabirds would move south in order to target discards from the CECAF demersal fleet. Nevertheless, the West African pelagic fishery has increased dramatically in the last forty years (Laurans et al., 2004), and targets the large shoals of mackerel *Trachurus* spp., pilchard *Sardina* spp., sardinella *Sardinells* spp., shad *Alosa* spp., and anchovy *Engraulis* spp. that congregate on the shelf break. A large pelagic

long-lining fleet also target the billfish (e.g. swordfish *Xiphias gladius*, sailfish *Istiophorus albicans*, and Atlantic marlin *Makaira nigricans*) that are drawn to these shoals (Lewison et al., 2004a, Zeeberg et al., 2006), and total pelagic landings across all CECAF divisions totalled more than 2.5 million tonnes in 2008 (FAO, 2010a). Seabirds may target the small quantities of discarded fish from these fleets, or be in competition with the vessels for the same resource (Bunce et al., 2002, Kelleher, 2004). An early study of seabird distributions observed during the Senegalese upwelling season (February-March 1976) reported sighting gannets, skuas *Stercorarius spp*., gulls *Larus spp.*, and terns *Sterna spp*., but suggested that this system was underexploited by seabirds (Brown, 1979). This pattern appears to have changed as, more recently, Camphuysen and van der Meer (2005) report that 40.1% of all birds observed during seabird surveys along the West African shelf break, 88.8% of all gannets (n = 2719) and 82.3% of all large gulls (n = 2973) were associated with fishing vessels.

The threat of fisheries bycatch

Despite the potential benefits of fisheries discards for seabird populations there are also negative effects and recent attention has been focused on issues surrounding bycatch (Lewison et al., 2004a, Lewison et al., 2009). Few data are available on the incidence of bycatch for many species, but it may be high: of the 24 extant albatross species, 21 have unfavourable conservation status attributed to bycatch mortality (IUCN, 2011). Bycatch may have drastic population level consequences, as the life-history strategies of marine megafauna make them vulnerable to increases in adult mortality, and this has been attributed to the decline of a number of marine vertebrates (Spotila et al., 2000, Tuck et al., 2001, Lewison and Crowder, 2003), including for example the near extinction of the barndoor skate *Raja laevis* (Casey and Myers, 1998).

The West African fleet present a major bycatch risk to marine vertebrates, and studies in this region reveal the bycatch of large numbers of pelagic billfish; hammerheads *Sphyrna spp.*; Requiem *Carcharinus spp*., mako *Isurus spp*., thresher *Alopias spp*., and blue *Prionace glauca*, sharks; manta ray *Manta birostris*, ray (*Dasyatidae, Rajidae*); ocean sunfish *Mola mola*; cetaceans, including short-finned pilot whales *Globicephala macrorynchus*, and a range of dolphin species (short-beaked common dolphin *Delphinus delphis*, bottlenose dolphin *Tursiops truncates*, white-sided dolphin *Lagenorhynchus acutus*); and three groups of sea turtle (leatherback *Dermochelys coriacea*, hawksbill *Eretmochelys imbricate*, and loggerhead *Caretta caretta*) (Zeeberg et al., 2006). However, the problem is not confined to large factory vessels. Small-scale and artisanal fisheries employ 99% of all fishers world-wide (Peckham et al., 2007) and are also known to produce high levels of bycatch (Peckham et al., 2007, Mangel et al., 2010). The threat posed to migratory seabirds in the Northwest African upwelling area is understudied, and accurately quantifying the threat of bycatch would require spatio-temporally resolved fishing data (Witt and Godley, 2007), but this is not widely or readily available. Moreover, using statistics such as landed tonnes per km^2 for large scale oceanic divisions does not take into account local-scale fishing effort or fish abundance, which vary widely (Witt and Godley, 2007). For coastal fisheries, disparities between data sources and a lack of spatial information make quantifying fishing effort difficult (Stewart et al., 2010). Recent work has also highlighted the risk from illegal unregulated and unreported fisheries (Pauly et al., 2002, Agnew et al., 2009), which may constitute an additional 40% of the reported West African catch (Agnew et al., 2009).

Protecting ecosystems

Despite wide-ranging behaviour, marine vertebrates are unlikely to be equally vulnerable across their entire range because anthropogenic pressures vary globally (Halpern et al., 2008). Protection could instead focus on areas of known importance (BirdLife, 2010b); such as breeding and foraging areas (Pichegru et al., 2010a), migration corridors (Shillinger et al., 2008), and wintering grounds (Phillips et al., 2005b). Recent evidence suggests individuals may show high fidelity to these areas (e.g. Alerstam et al., 2006, Broderick et al., 2007 and Chapter 4), and this could aid effective long-term protection (Shillinger et al., 2008). Predictive habitat modelling has enabled foraging movements to be linked with environmental factors (Louzao et al., 2010). Key to the effective protection of highly mobile species will be making marine protected areas (MPAs) ecologically relevant (Louzao et al., 2006), while setting boundaries to local geographically fixed features (i.e. bathymetry) will aide enforcement (Hyrenbach et al., 2006). Protection of relatively small pelagic areas can effectively protect the foraging grounds of highly mobile species (Hyrenbach et al., 2006), but marine vertebrates forage across dynamic pelagic systems (Weimerskirch, 2007) and will not be confined by pelagic MPA boundaries (Witt et al., 2008).

The Cape Verde population of loggerhead turtles operate exclusively within this region, making seasonal movements between the nesting beaches and West African waters. Hawkes et al.(2006) demonstrated age-structured migratory behaviour in this population, with older (larger) turtles foraging in coastal waters, while younger (smaller) turtles foraged neritically (over an area of more than half a million square kilometres). Therefore, not only is this population at risk from West African fleet throughout the annual cycle, but threats differ across age classes. Given this highly

vagile behaviour, conservation efforts will require international cooperation across seven African states (Hawkes et al., 2006)

The alternatives to MPAs

Pelagic MPAs are therefore not the only answer, and instead an ecosystem approach to fisheries management offers another avenue. The Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR) framework provides an example of management measures centred around: accurate reporting, gear regulations, bycatch limits, area and time restrictions, and mitigation measures (CCAMLR, 2010). Mitigation devices such as Brickle curtains, streamer lines, water cannons and Tori lines that exclude birds from around the hauling bay or scare birds from approaching during line setting, have dramatically reduced the bycatch of albatross and petrels in southern oceans longliner fleets (CCAMLR, 2008). For gill-net fisheries, acoustic pingers are effective at reducing cetacean and pinniped mortality; and in trawl fisheries, sea turtle excluder devices are effective at reducing sea turtle bycatch (Cox et al., 2007). However, all these measures require post-implementation monitoring to ensure continued compliance and effectiveness (Cox et al., 2007). Observer coverage is the most effective method for recording bycatch rates, but globally, current observer effort is low (Lewison et al., 2004b).

Conclusions

We need to prioritise conservation aims in order to minimise biodiversity loss (Brooks et al., 2006), and much of the oceans are impacted by some form of anthropogenic threat (Halpern et al., 2008). Population declines observed in one country may be due to events occurring elsewhere in the annual cycle, and so international co-operation is required to link populations and threats across international borders. We have

demonstrated here the importance of the Northwest African upwelling region for a broad range of species and age classes during the non-breeding period. Evidence from this and other studies suggests that current fishing practices in this region may have a detrimental impact on populations of marine predators, and pelagic MPAs provide one method to alleviate some of the anthropogenic pressures on marine ecosystems.

Chapter 6:
General discussion

This thesis has examined a range of the factors that may influence the marine spatial ecology of seabirds. In the following discussion I summarise the main findings of each chapter, highlight some of the issues faced while undertaking this project and set my findings in a wider context.

Potential impacts of offshore energy development

The marine environment is threatened by a number of anthropogenic pressures, and a range of sustainable (low carbon) methods of energy generation are required to limit reliance on dwindling fossil fuel reserves. The aim of **Chapter 2** was to build on the work of Inger et al. (2009, see Scientific contributions) and Gill (2005) who address potential ecological consequences for marine renewable energy, and focus specifically on the potential impacts of Marine Renewable Energy Installations (MREIs) on marine birds. MREIs will pose a range of both positive and negative impacts; negative impacts will include the threat of collision, both above and under water, and disturbance or displacement from particular areas; positive impacts may include habitat enhancement and protection. It is unclear what the overall impact of these effects may be. Previous work has considered the potential collision risk and barrier effects posed by offshore wind farms (Masden et al., 2009, Masden et al., 2010a, Masden et al., 2010b), but it is unlikely that wave-powered devices will have the same consequences due to their reduced profile in the water column. Nevertheless, as this industry develops it will become increasingly important to consider the spatial context of array design and location, especially with respect to other developments, but as yet there are only a handful of published field studies on wave-powered MREI impacts (Langhamer and

Wilhelmsson, 2009, Langhamer et al., 2009, Langhamer et al., 2010, Langton et al., 2011). Studies reviewing the biodiversity impacts of offshore wind farms have faced problems due to the difference in Environmental Impact Assessment (EIA) methodologies (Stewart et al., 2005, Stewart et al., 2007). Both the wave technology and environmental impact monitoring industries are in their infancy, and so the early adoption of common EIA methodologies is vital in order to prevent similar problems in the future.

The Wave Hub project is an offshore grid-connected facility located 16 km off the northern coast of Cornwall designed for the large-scale testing of wave energy conversion devices (www.wavehub.co.uk). To measure potential impacts at the Wave Hub site, a before-after-control-impact study began in August 2008, carrying out monthly biodiversity surveys to monitor the abundance of seabirds, cetaceans and pinnipeds. The intention of this was to build up a comprehensive baseline dataset, using visual surveys, acoustic monitoring and environmental sampling to monitor spatial and temporal trends both pre- and post-development. Unfortunately however, it has not been possible within the scope of this study to expand beyond this initial baseline: as of May 2011 the devices are still to be installed. Nevertheless, key to the success of MREI control studies will be the early adoption of appropriate survey methodologies, and our Wave Hub case study now has a long-term multi-season baseline with which to compare any potential device effects.

Highlighting important foraging areas during the breeding season

Understanding the spatial context of anthropogenic threats requires an understanding of the spatial distribution of seabirds. During the breeding season many seabirds act as central-place foragers, and this restricts the way in which they exploit the marine

environment. The work in **Chapter 3** began as a scoping exercise, to highlight those species whose foraging ranges may overlap with the Wave hub site during the breeding season. I developed this modelling projection framework into a single species model, using the northern gannet *Morus bassanus* (hereafter gannet) as a model organism, and synthesised information from colony surveys with detailed information on population dynamics, foraging ecology and near-colony behaviour.

Tracking data provides fine-scale information on the movements of individuals (Votier et al., 2010), and can be linked with remotely sensed environmental variables to better understand foraging ecology (Louzao et al., 2010); however, this approach is not always possible. Colonies are often inaccessible, or species are unable to carry tracking devices due to size limitations (Phillips et al., 2003, Barron et al., 2010). The gannet is a useful model in this case because it is well studied, has been tracked from a number of colonies (Grémillet et al., 2006, Hamer et al., 2009, Votier et al., 2010), and is conspicuous during at-sea surveys (Kober et al., 2010). The projection models revealed very similar patterns to those described by tracking data and at-sea surveys (i.e. Kober et al., 2010), suggesting that this relatively simple approach is useful for predicting the at-sea distribution of seabirds during the breeding season. This technique could therefore provide a framework with which to project the foraging ranges of other species traditionally hard to detect at-sea, or those species that are too small or sensitive to track. Attention is now focussed on establishing a network of Marine Protected Areas (MPAs) for seabirds (Reid and Webb, 2005, Wilson et al., 2009, Kober et al., 2010) and this approach offers a timely method to highlight important pelagic habitats for seabirds. Moreover, this approach could also be used to address theoretical questions regarding the role of intra-specific competition in shaping seabird population dynamics, and could be easily adapted for other central-place marine predators such as pinnipeds.

Examining migratory strategies and seabird ecology in detail

As highlighted above, steps are being made to protect seabirds during the breeding season, but we have a limited understanding of the role that the non-breeding period has for individual life-history strategies. To try and understand this better, the main field-based aspect of this project has centred on two species, the gannet and the lesser black-backed gull *Larus fuscus*. At the outset, our aim was to focus on two colonies, Grassholm, Pembrokeshire (51.730°N, 5.486°W) for gannets, and Gugh, Isles of Scilly (49.891°N, 6.330°W) for lesser black-backed gulls. Colony-based studies monitoring foraging behaviour, diet, body condition and breeding success would be combined with the tracking of individuals through the non-breeding period, and allow the potential consequences of individual variation in migratory strategy to be studied (Furness et al., 2006). These two species are also capable of foraging within the confines of the Wave Hub site (Figure 1.1) and so would provide useful models to examine any potential impacts of the Wave Hub development. Both of these species are paramount to UK conservation efforts, as Britain and Ireland together hold circa 60-70% of the global populations of gannets, and the *graellsii* sub-species of the lesser black-backed gull *Larus fuscus graellsii*. This study further developed to include a collaboration with David Grémillet (CNRS, France) who provided access to Rouzic, the only French gannet colony (48.900°N, 3.436°W).

In **Chapter 4** I combine information on the migratory strategies of gannets from both the Grassholm and Rouzic colonies. This chapter used two complementary techniques that, despite their popularity, have only rarely been used in combination; geolocation sensors to provide information on long-distance and long-term movements of individuals, and stable isotope analysis to provide information on the dietary preferences of individuals during the non-breeding period. Combining these two

approaches provided an insight into the migratory and foraging patterns of gannets from two important colonies. Gannets demonstrated extreme levels of fidelity to particular wintering areas and showed consistent isotopic signatures across years. Winter philopatry and foraging consistency have been found in a wide range of marine vertebrates (Bearhop et al., 2000, Bradshaw et al., 2004, Phillips et al., 2005b, Phillips et al., 2006, Broderick et al., 2007, Woo et al., 2008, Newsome et al., 2009, Hawkes et al., 2011), but this study was among the first to describe potential consequences of these strategies (but see Zbinden et al., 2011).

High individual consistency would allow individuals to target persistently productive regions during the winter period, and the adoption of individual migratory and foraging specialisations would mitigate competition during the non-breeding period. However, consistency may be maladaptive if it were to increase the vulnerability of individuals to threats in these locations, or prevent them from switching to new environments in the face of change. Recent studies have demonstrated flexibility in the migratory strategies of Cory's shearwater (Dias et al., 2011) and suggest that this will allow the population to respond quickly to environmental change. Only two of the gannets tracked in this study had centres of wintering distributions that moved between seasons, from the Mauritanian coast in 2008/09 to southern Morocco in 2009/10.

This study demonstrates the importance of the non-breeding period as a key element of the gannets' life-history strategy, and highlights the need to incorporate protection of the wintering grounds into conservation legislation. An estimated 70% of the global breeding population of northern gannets spend the breeding period in UK, Irish, and French waters (Nelson, 2002, Mitchell et al., 2004, Grémillet et al., 2006), and so

ensuring adequate protection of gannets during the non-breeding period is paramount to European conservation efforts.

The contrasting fates of urban and rural nesting lesser black-backed gulls

Although not reported in this thesis, part of the reason for the lesser black-backed gull project was to better understand the contrasting fortunes of two different UK populations; while rural colonies, such as those on the Isles of Scilly, have been declining in recent years, urban populations are rapidly increasing in cities such as Bristol and Gloucester. For gulls, the urban environment can offer readily accessible food resources (in the form of anthropogenic waste), provide large numbers of potential nest sites, higher ambient temperatures, and a low or complete absence of predators. Interestingly, there appears to be little movement of ringed adults between urban and rural populations, and so these may represent two very different strategies.

I trapped adult gulls nesting on roofs in Bristol and Gloucester in 2009, deployed geolocators to examine wintering strategies, sampled blood and feathers for isotope analysis, measured a number of body condition indices, and recorded clutch volumes as a measure of parental investment. However, the nesting density of birds in urban areas is much lower than at rural colonies, and individuals are more wary. This resulted in only 8 geolocators being deployed across Bristol and Gloucester compared to 20 deployments at the Gugh colony on the Isles of Scilly. Furthermore, retrieving devices in 2010 was impossible; the few birds that did return either did not breed, or were actively prevented from doing so by landowners. Nevertheless, initial results were interesting; adults nesting in urban areas tended to be in better condition than their rural counterparts ($t = -2.057$, $df = 10.686$, $p = 0.065$), but showed no differences in clutch volume.

The importance of particular wintering areas and the case for pelagic MPAs

In **Chapter 5** I examined the range of threats that five important marine vertebrates may be exposed to during the non-breeding period by focusing on one key wintering hotspot; the Northwest African upwelling region. The combination of the seasonal Moroccan and Senegalese upwellings, and the permanent Mauritanian upwelling produced by the Canaries Current, make the waters along the Northwest African coast a hotspot of marine biodiversity (Brown, 1979, IUCN, 1989, Camphuysen and van der Meer, 2005), and supports globally important wintering aggregations of gannets, lesser black-backed gulls, loggerhead turtles *Caretta caretta* (Hawkes et al., 2006), great skuas *Stercorarius skua* (Furness et al., 2006), and Cory's shearwaters *Calonectris diomedea* (González-Solís et al., 2007).

This region is also under pressure from anthropogenic threats, including an expanding international fishery and offshore mineral extraction (Camphuysen and van der Meer, 2005, Worm et al., 2009). The Northwest African pelagic fleet has increased dramatically over the last four decades, and appears to be in direct competition with the marine vertebrates that winter in this area, as both target the large shoals of pelagic fish that congregate on the shelf break. This fleet has an extremely high bycatch rate; catching a range of species from sunfish *Mola mola* to pilot whale *Globicephala macrorynchus* (Zeeberg et al., 2006). Combining information on the non-breeding distributions of five marine vertebrate species demonstrates the importance of this area for a range of species and age classes. It is unlikely that marine vertebrates can co-exist with fisheries when current fishing practices are considered. Pelagic MPAs present a vital tool to mitigate these impacts, and the data collated in this chapter could provide the foundation for justifying the Northwest African upwelling as a region in need of protection.

Summary

Further work needs to focus on the impact of anthropogenic threats in the marine environment and, when possible, developments should be designed with positive biodiversity impacts in mind. When data is lacking, or unavailable at large scales, modelling techniques can be used successfully to highlight foraging areas of importance for breeding seabirds. In turn, these can be used to inform protection, and mitigate developments. It is also important to consider the scale at which many apex predators utilise the marine environment, as during the breeding season many species travel large distances from discrete colonies to forage. As a result, offshore activities such as energy generation, mineral extraction and commercial fisheries can have impacts at colonies many kilometres away.

Conditions during the non-breeding period carry-over to impact individuals during the breeding period, and so the non-breeding period is paramount to individual fitness. It is therefore inadequate to protect just the breeding grounds of individuals, as they represent a relatively small portion of the annual cycle. Work is required to establish a network of pelagic MPAs that protect the key wintering areas of migratory species and complement existing protection at breeding grounds. This process can be informed by the combined use of colony-based studies, bio-logging, stable isotope analysis and modelling techniques that provide a comprehensive understanding of the interactions between individuals and the marine environment over multiple spatial and temporal scales.

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